

Assembly of plant communities in fragmented landscapes:

The role of dispersal

Wim A. Ozinga

Assembly of plant communities in fragmented landscapes:

The role of dispersal

Een wetenschappelijke proeve op het gebied van de Natuurwetenschappen,
Wiskunde en Informatica

PROEFSCHRIFT

ter verkrijging van de graad van doctor
aan de Radboud Universiteit Nijmegen
op gezag van de Rector Magnificus prof. mr. S.C.J.J. Kortmann,
volgens besluit van het College van Decanen
in het openbaar te verdedigen op
dinsdag 15 januari 2008
om 15.30 uur precies

door

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geboren op 16 augustus 1971
te Utrecht

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ISBN: 978-90-9022584-5

Lay-out and figures: Dick Visser

Printed by: Van Denderen BV, Groningen

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Ozinga, W.A. (2008) Assembly of plant communities in fragmented landscapes:
The role of dispersal. PhD thesis, Radboud University Nijmegen.



The research presented in this PhD thesis was financially supported by the Netherlands Organisation for Scientific Research (NWO), project nr. 014.22.072.

Contents

Abstract	7
Introduction	
Chapter 1. General introduction	9
Box 1: A new tool in the search for community assembly rules: ecoinformatics	24
Box 2: Plant community types in the Netherlands within a habitat template	26
Chapter 2. Classification of dispersal traits of vascular plants	31
Dispersal limitation versus environmental constraints	
Chapter 3. Predictability of plant community composition from environmental conditions is constrained by dispersal limitation. (<i>Oikos</i> 108: 555–561, 2005)	53
Chapter 4. Local aboveground persistence of vascular plants: Life-history trade-offs and environmental constraints. (<i>Journal of Vegetation Science</i> 18: 489–497, 2007)	65
Chapter 5. Dispersal potential in plant communities depends on environmental conditions. (<i>Journal of Ecology</i> 92: 767–777, 2004)	83
Dispersal traits versus stochastic dispersal	
Chapter 6. Assessing the relative importance of dispersal in plant communities using an ecoinformatics approach. (<i>Folia Geobotanica</i> 40: 53–68, 2005)	101
Dispersal problems due to human interference	
Chapter 7. How important is long-distance seed dispersal by wind for regional survival of plant species? (<i>Diversity and Distributions</i> 11: 165–172, 2005)	117
Chapter 8. Availability of dispersal vectors as a key to plant losses in NW Europe. (submitted)	131
Box 3: Overview of changes in dispersal infrastructure in the Netherlands.	145
Synthesis and applied perspectives	
Chapter 9. The role of dispersal in the assembly of plant communities	151
Chapter 10. Restoration of dispersal processes in fragmented landscapes	163
References	187
Summary	213
Samenvatting	219
Dankwoord / Acknowledgment	233
Curriculum Vitae	237

Abstract

Ozinga, W.A. (2008) Assembly of plant communities in fragmented landscapes: The role of dispersal. PhD thesis, Radboud University Nijmegen.

The present research showed that dispersal problems in fragmented landscapes are as important for the understanding of plant diversity losses as the traditional explanation of deteriorating habitat quality.

Efficient conservation and restoration of plant diversity requires a predictive ecology based on general principles of the assembly of plant communities (so-called 'assembly rules'). Theories on the processes that shape local plant communities can be grouped into three broad views according to the main processes involved: niche-based processes, dispersal-based processes and trait-neutral, abundance-driven processes. The present research combined large databases with information on community composition and functional traits to compare the predictive power of these three views of community assembly.

Although species were found to clearly sort along environmental gradients (niche-based processes), our results indicate that for most species the availability of seeds is a major limiting factor. This 'seed limitation' has two components: the limited availability of seed sources (trait-neutral, abundance-driven processes) and the limited transport of the available seeds (dispersal-based processes). This thesis documents the impact of 'seed limitation' across several levels of organization (species, community, landscape).

We showed that differences between plant species in terms of adaptations to various modes of transport are a key factor in understanding losses of plant diversity in Northwest Europe in the 20th century. Species with water- or fur-assisted dispersal are over-represented among declining species, while species with wind- or bird-assisted dispersal are under-represented. This implies that past changes in the 'dispersal infrastructure' are at least as important in explaining diversity losses as the conventional explanation of environmental change. Traditional niche-based conservation measures, although useful, are thus not enough to halt diversity losses. We propose measures to restore the 'dispersal infrastructure' across entire regions.

Keywords: Coexistence; Community assembly; Dispersal limitation; Ecoinformatics; Habitat fragmentation; Functional traits; Land-use changes; Metacommunity; Neutral theory; Niche; Seed limitation; Species pool; Trait–environment linkages

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General introduction

Species-rich dune grassland with Early Marsh-orchid (*Dactylorhiza incarnata*).

“The development of ecology as a rigorous predictive science now depends upon our success in recognising principles of wide generality and avoiding submergence in the rising flotsam of case studies, specialist observations, and untested theories.”

Grime 2001

Halting the biodiversity crisis: the need for a predictive ecology

The biodiversity crisis

All over the world, biodiversity is declining at an alarming rate, which is unprecedented except for a few periods of mass extinction (Lawton & May 1995, Pimm et al. 1995, Millennium Ecosystem Assessment 2005). This probably also applies to vascular plants, which are the organisms this thesis focuses on. In Europe, for example, approximately 20% of the vascular plant species are classified as globally threatened according to IUCN criteria, and this is a conservative estimate, since for many rare endemic species the threat status has not been estimated at all (Walter & Gillett 1998, Ozinga & Schaminée 2005, IUCN 2006). The main drivers of biodiversity loss are habitat loss and reduction of the quality and spatial coherence of the remaining habitat patches (Millennium Ecosystem Assessment 2005).

Growing concern about the ongoing loss of biodiversity has resulted in increased efforts for the protection of endangered species and for the conservation and restoration of endangered ecosystems throughout the world (Schemske et al. 1994, United Nations 2002, Delbaere 2002, Balmford et al. 2005). Whereas nature conservation measures are being implemented all over the world to maintain existing biodiversity, ecological restoration is practised mainly in highly industrialized countries in Europe and North America (Hobbs & Norton 1996, Bakker 2005, Van Andel & Aronson 2006). Ecological restoration aims to develop impoverished human-dominated ecosystems into semi-natural systems in which natural processes play a more prominent role (Hobbs & Norton 1996, Bakker & Berendse 1999, Van Andel & Aronson 2006). In practice, ecological restoration aims at directing ecosystems along desired successional trajectories by measures that accelerate succession or short-cut successional stages (Lockwood & Pimm 1999, Bakker et al. 2000).

Ecological restoration projects in Europe and North America have mainly focused on restoring abiotic conditions. Although there have been various local successes, the resulting vegetation developments have in many cases been disappointing in terms of plant diversity, especially as regards endangered species (Dobson et al. 1997, Bakker & Berendse 1999, Bekker & Lammerts 2002, Jansen et al. 2004).

Disappointing results are partly the consequence of changes in chemical, physical and biological properties of the organic topsoil after long-term drainage, pollution or intensive fertilization, which are more difficult to reverse than was once hoped (Grootjans et al. 2002, Roelofs et al. 2002, Lucassen et al. 2005). In recent years, ecologists have therefore begun to question whether ecological restoration is actually effective for biodiversity conservation purposes, or whether it merely means replacing one degraded system by another (Dobson et al. 1997, Suding et al. 2004, Hodgson et al. 2005).

Accumulating evidence suggests that even if abiotic conditions can be sufficiently restored, the degree to which endangered plant species re-colonize the restored area is often small, due to habitat fragmentation (e.g. Hutchings & Booth 1996, Bakker & Berendse 1999, Lockwood & Pimm 1999, Verhagen et al. 2001, Jacquemyn et al. 2003). It is therefore increasingly acknowledged that the availability of seeds can also be a major limiting factor ('seed limitation') in ecological restoration projects (Strykstra et al. 1998, Bakker & Berendse 1999, Turnbull et al. 2000, Ehrlén & Eriksson 2000, Mouquet et al. 2004). Seed limitation can be defined as the failure to establish a new population or increase the size of an existing population without seeds being added (Turnbull et al. 2000).

It is therefore important for efficient restoration efforts to have reliable indications of the degree to which the absence of certain endangered species might be explained by seed limitation or by other limiting factors (constraints). In other words: it is necessary to differentiate between sites that are unsuitable for the establishment of species from an environmental perspective and sites that are suitable but as yet unoccupied (Freckleton & Watkinson 2002, Münzbergová & Herben 2004, Ozinga et al. 2005).

The need for a predictive ecology

In view of the large input of financial and human resources in nature conservation and restoration, we need to know more about the relative importance of mechanisms that determine the species composition of communities. This can be regarded as one of the major scientific challenges for the coming decades, if we are to formulate appropriate conservation and restoration strategies.

From the perspective of ecosystem functioning, there is a growing awareness that it is not the number of species as such which is important, but rather the composition of plant properties (traits) (Grime 2002, Díaz & Cabido 2001, Díaz et al. 2004, Hooper et al. 2005, Spehn et al. 2005, Thompson et al. 2005, Van Ruijven & Berendse 2005). A trait can be defined as a well-defined, measurable property of an organism that is used comparatively across species. To be useful for predictions about community assembly, traits should vary more between than within species (McGill et al. 2006). Species traits are assumed to represent evolutionary adaptations to the physical and biological environment of a species (Ackerly 2003). Each species is thus characterized by a certain set of trait states (attributes). A *functional trait* is one that strongly influences the performance of

organisms within an ecosystem (cf. McGill et al. 2006, Violle et al. 2007). It is therefore of paramount importance that our understanding of species richness patterns is supplemented by a better understanding of mechanisms that drive patterns in trait composition. Understanding these mechanisms will provide us with the ‘assembly rules’ (cf. Diamond 1975) of plant communities and will result in a more predictive ecology.

Three views of community assembly

There is currently a wealth of theories on the major processes that shape the species composition of local plant communities. These theories can be grouped into three broad views, according to the main processes involved. These three views of the building of communities (community assembly) are ranked below in decreasing order of predictive power as regards species composition.

- *Niche-based view*, in which suitability of the local environment is the main limiting factor. This view is based on spatial and temporal heterogeneity in environmental conditions (both abiotic and biotic) in combination with differences between species in exploiting these conditions.
- *Dispersal-based view*, in which dispersal is the main limiting factor. This view is based on regional dynamics of habitat patches in combination with differences between species in their ability for dispersal in space and time.
- *Trait-neutral view*, in which the availability of seed sources is the main limiting factor. This view is based on stochastic processes in which the probabilities are determined by the abundance of species in the species pool.

Niche-based view of community assembly

The niche-based view is based on functional differences between species in terms of competitive ability, stress tolerance and resistance to disturbance (e.g. Hutchinson 1961, Grime 1977, Tilman 1985, Ellenberg 1988, Berendse et al. 1992, Keddy 1992, Grace 1999, Silvertown 2004). Spatial and temporal heterogeneity in environmental conditions (both abiotic and biotic) then results in niche segregation between species and in the sorting of species along environmental gradients, both between and within habitats. This allows long-term co-existence by minimizing the strength of competitive interactions between species. In this ‘niche assembly view’, the species composition of a community is thus a deterministic consequence of physiological processes and biological interactions, given a specific set of environmental conditions.

At the species level, these niche-based processes result in predictable occurrences of species along environmental gradients. The niche of a species can be

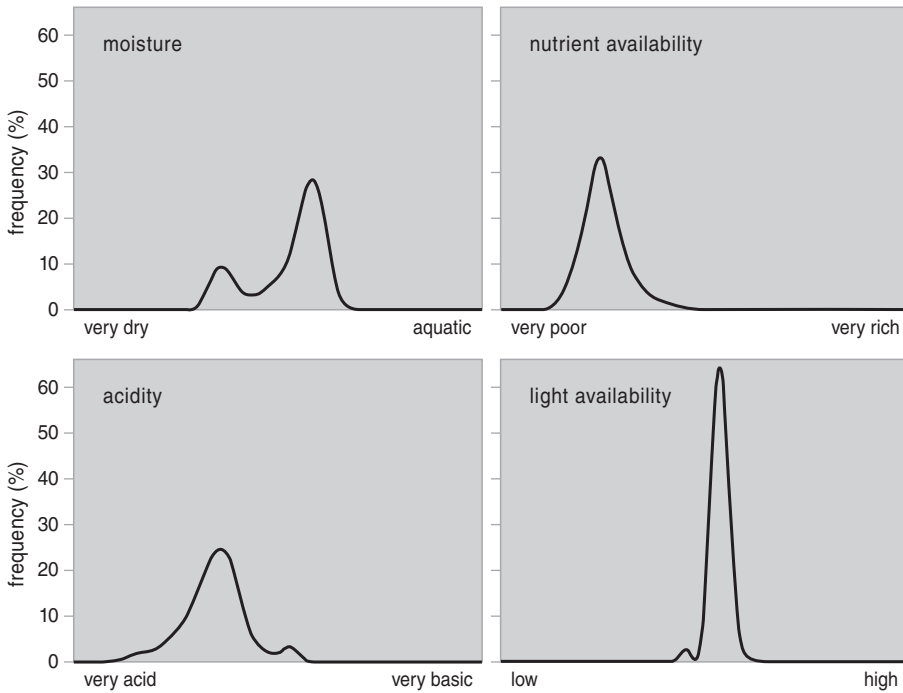


Figure 1.1: Components of the realized niche of the grassland herb Devil's bit Scabious (*Succisa pratensis*) quantified by its frequency of occurrence along four environmental gradients (the x-axes represent four 'niche axes' based on mean Ellenberg indicator values per plot). The y-axis gives the normalized frequency in percentages based on 575 occupied plots (based on Ozinga & Schaminée 2004).

defined as the ecological conditions that allow a species to satisfy its minimal requirements so that the rate of reproduction of a local population is equal to or greater than its death rate (Chase & Leibold 2003). In practice, niches are identified by the frequency of occurrence of species along environmental gradients (Silvertown 2004, Austin 2005; see Fig. 1.1). The set of response curves along the major environmental gradients can be regarded as an aggregated measure of the realized niche (cf. Persson 1981, Ellenberg 1988, Silvertown 2004, Austin 2005). The sorting of a number of species along environmental gradients then results in distinct spatial differences in local species composition (see also Box 2).

Classical niche-based theory is able to predict the occurrence of species along environmental gradients to a certain degree, but a major limitation is that it does not provide a general explanation for the relative abundance of species within habitat types, either at the local or at the regional scale. Most habitats are characterized by just a few frequent species that occur in most sites, so-called 'core species' (cf. Hanski 1982) and a long tail of less frequent species, so-called 'satel-

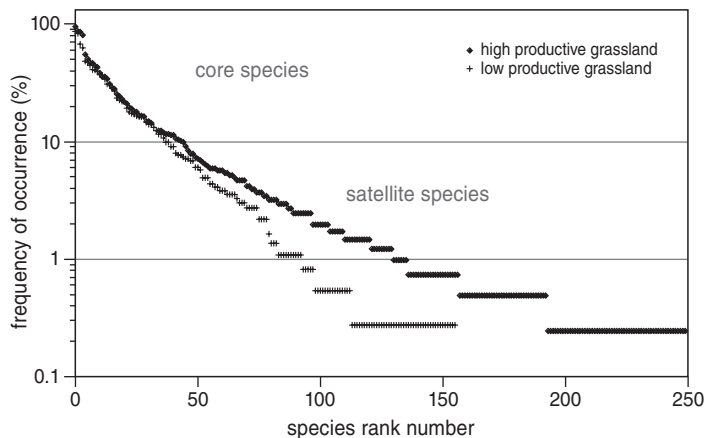


Figure 1.2: Rank – abundance curve (Whittaker 1965, Magurran 2005) for two grassland community types: a highly productive wet grassland (*Ranunculo-Alopecuretum*) and a low-productive, dry grassland (*Spergulo-Corynephoretum*). The X-axis gives the rank number of the species, while the Y-axis gives the relative abundance expressed as the percentage of occupied plots (N=500 plots; note the log-scale). Both community types contain just a few common species that occur at the majority of sites (core species), and a long tail of rare species (satellite species).

lite species' (see Fig. 1.2). At regional scale, common species thus dominate the landscape by their large number of individuals, while less frequent species make up the majority of species numbers and thus determine biodiversity (Preston 1948, 1962, Whittaker 1965). For the conservation of plant diversity, it is therefore important to know which processes determine the relative abundance of species in terms of frequency of occurrence. This limitation of the niche-based view therefore calls for a complementary approach.

Dispersal-based view of community assembly

In contrast to the niche-based assembly view, with its focus on local interactions, the dispersal assembly view focuses on larger spatial and temporal scales, and was inspired by MacArthur and Wilson's (1967) theory of island biogeography and by its modern successor, metapopulation theory (e.g. Levins 1969 and Hanski 1998). The metapopulation perspective involves an explicit recognition of scales, and an explicit distinction between within-patch (local) and among-patch (regional) dynamics (Levin 1992). In traditional plant ecology, the prevailing notion was that plant species occupied all suitable habitats within a landscape (Bullock et al 2002). Metapopulation theory predicts that for a given plant species, only a fraction of suitable habitat patches are actually occupied, because species continually become extinct on a local scale (<100m²) and the dispersal ability of most (if not all) species is expected to be limited, at least at larger spatial scales (Levins

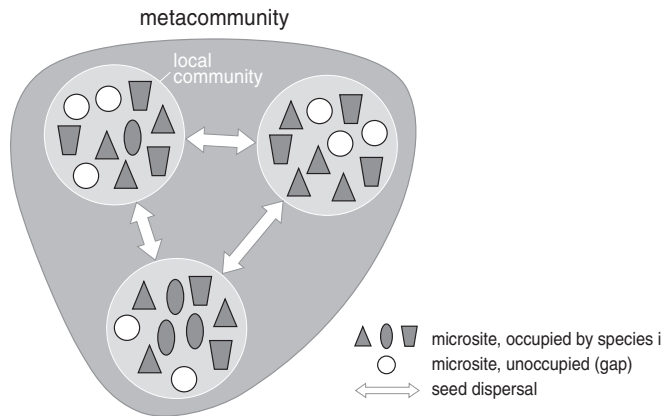


Figure 1.3: Visualization of the three scale levels in the metacommunity concept. At the smallest scale, microsites can hold a single individual. Microsites are nested within localities (habitat patches) that hold local communities. Local communities are separated from each other by areas with other habitat types and are connected to each other by seed dispersal as part of a metacommunity occupying a region. In theory, differences in connectivity between sites (affecting the rate of seed dispersal), together with species-specific differences in dispersal ability, might explain the variation in species composition across local communities.

1969, Eriksson 1996, Hanski 1998, Turnbull et al. 2000). Regional persistence of species therefore entails colonization of unoccupied sites (Olivieri 1995, Hanski 1998). In metapopulation theory, the probability of local occurrence of species is described as a dynamic equilibrium between colonization and local extinction (MacArthur & Wilson 1967, Hanski 1982, 1998).

Indeed, many empirical studies have shown that there is a continuous small-scale turnover of plant species (Watt 1947, 1960, Van der Maarel & Sykes 1993, Sykes et al. 1994, Herben et al. 1997, Klimeš 1999, Palmer & Rusch 2001), the net result being that plant species show temporal variation in their spatial distribution patterns, like shifting clouds in the sky (Grubb et al. 1982).

In the dispersal assembly view, traits that determine a species' dispersal ability in space (long-distance dispersal) and / or in time (accumulation of a persistent soil seed bank) can be expected to influence the dynamic balance between colonization and local extinction (Grime & Hillier 1992, Tilman 1994, 1997, Ehrlén & Van Groenendael 1998, Eriksson 2000, Turnbull et al. 2000, Foster et al. 2004, Fenner & Thompson 2005, Ozinga et al. 2005). In theory, this may then translate at the community level into differences in local species composition between plots with the same environmental conditions. However, the relative importance of interspecific differences in dispersal ability for the assembly of local communities remains to be convincingly demonstrated (Levine & Murrell 2003, Etienne & Alonso 2005, Harpole & Tilman 2006, Purvis & Pacala 2005).

Most studies on seed dispersal have focused on single plant species or limited sets of species, and far less is known about the effects of seed limitation on community composition. In recent years, attention has therefore started to shift from metapopulations towards so-called metacommunities or even meta-ecosystems (cf. Loreau et al. 2003). The dispersal assembly view can be regarded as a trait-based extension of metapopulation theory to the level of ‘metacommunities’.

A *metacommunity* can be defined as a set of local communities (with potentially interacting species belonging to the same trophic level) that are connected by the dispersal of component species (Wilson 1992, Hubbell 2001, Mouquet & Loreau 2002, Leibold et al. 2004). However, unlike species in local communities, species in metacommunities may not actually interact with each other because the local communities may be separated in space or time. Many models of metacommunity dynamics are based on a three-level hierarchy (Hubbell 2001, Leibold et al. 2004; see Fig. 1.3). (1) At the smallest scale, microsites can hold a single individual. (2) Microsites are nested within localities (habitat patches) that hold local communities. (3) Local communities are separated from each other by areas with other habitat types and are connected to each other by dispersal as part of a metacommunity occupying a region.

Trait-neutral view of community assembly

In contrast to the two above views of community assembly, the ‘trait-neutral view’ is not based on differences between species in terms of their functional traits. Trait-neutral models assume that interspecific differences in plant properties (traits) are not important at all in determining species abundance patterns as expressed by their frequency of occurrence (Hubbell 1997, 2001, Bell 2001). Species are regarded as functionally equivalent in the sense that they have identical rates of birth, death, dispersal and speciation on a per capita basis (Hubbell 2001). The trait-neutral view thus approaches community assembly from the opposite direction as compared to the other two views, by asking: How many of the patterns of ecological communities are the result of species similarities, rather than of species differences? (Hubbell 2006).

The trait-neutral view is neutral in the sense that individuals, and thus species, are regarded as ecologically equivalent in terms of competitive ability and dispersal ability. Patterns in relative species abundance (frequency of occurrence) are explained solely from random dispersal, random fluctuations in birth and deaths, and genetic drift. The most important way in which species differ, according to Hubbell (2001), is in their relative abundance in the metacommunity, and this strongly affects their probability of extinction and colonization. Species are thus common or rare purely by chance, and relative abundance patterns are a historical accident in this view.

Although the existence of interspecific differences in dispersal ability and local persistence is well established (see above), this does not necessarily mean that these differences affect local species composition. Hubbell (2001) and Volkov

et al. (2003) give examples from tropical forests in which the trait-neutral model performs surprisingly well in describing patterns of relative abundance of species within and across communities, and neutral theory is regarded by some authors as one of the most exciting conceptual advances in ecology in decades (Abrams 2001, Tilman 2004, Etienne & Alonso 2005, Magurran 2005, Pandolfi 2006).

The critical question is thus not whether competition or dispersal is the important process, but whether differences in functional traits between species translate into differences in local species composition. In other words: do interspecific differences matter? Hubbell's model can therefore serve as a powerful 'null model' for testing the effects of non-random, trait-based processes (cf. Connor & Simberloff 1979, Gotelli 2000, 2001, Harte 2004, Tilman 2004, Etienne & Alonso 2005). In this thesis, the trait-neutral view is used as such. If the null model (based on the abundance of species in the regional species pool) can successfully explain the data, there is no compelling reason to go beyond it to seek further explanations based on functional traits. If so, this would imply that species composition is inherently unpredictable.

Prerequisites for a predictive ecology based on functional traits

Empirical evidence for the operation of trait-based assembly rules, taking into account trait-neutral abundance-based processes, is still surprisingly limited (Levine & Murrell 2003, Etienne & Alonso 2005, Harpole & Tilman 2006, Purvis & Pacala 2005, Alonso et al. 2006, Adler et al. 2007). Nevertheless, it is important, both from a theoretical and an applied perspective, to develop a predictive ecological theory based on differences between species in functional traits, if such a theory can indeed be developed. This requires that incorporating such traits can be demonstrated to yield a substantial improvement in predictive power of the model for local community assembly from a regional species pool, compared to a trait-neutral null model using only differences in relative regional abundance. To demonstrate this, three (interrelated) questions need to be addressed:

- What is the relative importance of niche-related traits and dispersal-related traits in predicting the presence or absence of species in local communities from the pool of regionally available species (i.e. which filters and traits are involved in the assembly of plant communities)?

If it is indeed possible to identify such filters and traits, one could look for correlations among variables that facilitate the interpretation of community assembly:

- Are there negative correlations between functional traits which a plant cannot optimize simultaneously (trade-offs), leading to trait syndromes?
- Are there correlations between functional traits and the major ecological gradients?

What is the relative importance of niche-related and dispersal-related processes for the assembly of plant communities?

Jared Diamond (1975) proposed that the search for the generalities that underlie the building of local communities from the pool of available species can be approached conceptually by defining so-called '*community assembly rules*'. These assembly rules can be regarded as a set of 'filters', with each filter representing a major ecological limitation (constraint) on the assembly of communities (see Fig. 1.4). These filters admit or exclude species from the total species pool according to their functional attributes (Diamond 1975, Southwood 1988, Keddy 1992, Díaz et al. 1998, 1999, Kleyer 1999, Weiher & Keddy 1999, Grime 2001, 2006). Filters thus operate on traits (with their corresponding trait states or attributes), rather than on plant species. The challenge to community ecology is then to quantify the key filters involved and subsequently to identify the relevant traits.

Are there trade-offs between functional traits?

Traits themselves might be related to each other by interspecific trade-offs which reflect the simple fact that resources allocated to one structure cannot be allocated to another structure (e.g. Harper et al. 1970, Grime 1977, 2001, Grubb 1977, Southwood 1988, Tilman 1990, Díaz et al. 2004, Kneitel & Chase 2004). Negative correlations between two traits, however, do not necessarily imply a mechanistic connection between these traits but may also result from shared evolutionary functions because the existence of one trait might reduce the adaptive value of the other. Irrespective of their cause, negative correlations between traits restrict parameters (trait states or attributes) to a limited part of the possible multidimensional 'trait surface' (Grime 1977, Southwood 1988, Tilman 1990) and as a result also limits the available options for the 'functional response' of species. The resulting combinations of attributes can be regarded as 'trait syndromes' or 'strategies' which represent alternative solutions to the problems posed by environmental constraints (Grime 1977, 2001, Lavorel et al. 1997).

What is the dispersion of functional traits along the major ecological gradients?

Once the major ecological constraints are known, together with the relationships between traits, the predictability of community assembly depends on the degree to which it is possible to map recurrent patterns of traits along the ecological gradients. The relative abundance of trait syndromes is expected to vary across ecological gradients, given the existence of trade-offs, because traits of a species that increase its fitness in response to one suite of ecological conditions should have a cost that decreases its fitness under other conditions (Grime 1977, 2001, Grubb 1977, Connell 1978, Tilman 1990). Ecological constraints thus impose restrictions on the viable trait combinations in a given habitat (Tilman 1990, Grime 2001, 2006, Kneitel & Chase 2004), and the major ecological gradients can be used as a kind of template to map traits (Southwood 1988, Keddy 1992, Ackerly 2003).

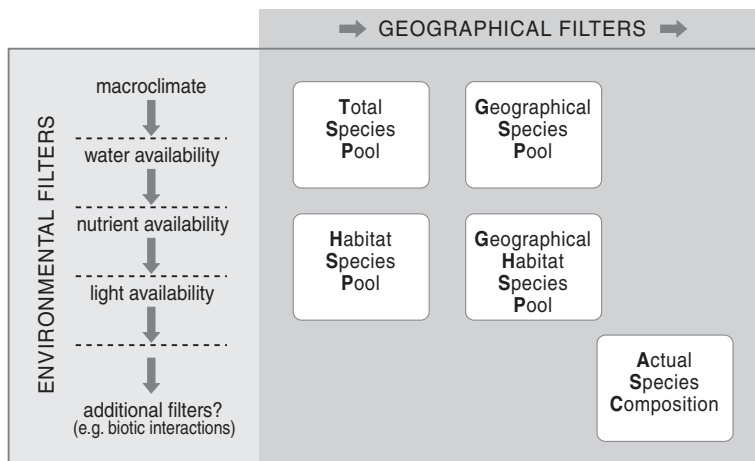


Figure 1.4: Conceptual model of the major constraints that act on a given species pool and result in the actual species composition of a local community. The constraints operate as environmental filters (niche-based assembly) and isolation filters (dispersal assembly) on the total species pool (from Ozinga et al. 2005a; see Chapter 6).

Once these three questions have been addressed, functional traits can be used to try and explain the presence or absence of species in a local community under the prevailing set of environmental or spatial constraints. If functional traits do indeed have predictive power for community assembly, then the importance about knowledge of functional attributes of individual plant species can hardly be overestimated in designing restoration programmes (see Chapter 10). The focus on traits, rather than taxa, allows ecological predictions beyond context-specific case studies. By contrast, if trait-neutral stochastic processes prevail in community assembly, a more predictive ecology will remain illusive.

Human interference with community assembly

The need for a predictive ecology is most strongly felt in the industrialized part of the world, where it could be the basis for mitigation and restoration measures. Intensive human land use in these regions leads to habitat loss and to changes in the quality and configuration of the remaining habitats, as well as changes in dispersal processes. Changing land use therefore affects both niche-based processes and dispersal processes. Our understanding of human interference with assembly processes and their relative importance is, however, very incomplete. Or, in the words of Vitousek et al. (1997), ‘we are changing the earth more rapidly than we are understanding it.’

Deterioration of habitat quality

Humans began influencing habitat conditions in Europe from the period of the first agricultural immigrations onwards (ca. 7000 yr. BP). The resulting semi-natural landscapes supported high diversities of plant and animal species (Waterbolk 1968, Westhoff 1983, Ellenberg 1988, Lohmeyer & Sukopp 1992). The mechanization of agriculture in the 20th century, with deep ploughing, drainage and the application of artificial inorganic fertilizers, greatly altered habitat conditions and thereby changed the species composition of many semi-natural habitat types (Westhoff 1983, Ellenberg 1988, Grootjans et al. 1996, Schaminée et al. 2002, Bakker 2005, European Environmental Agency 2005).

Habitat deterioration due to eutrophication is regarded as one of the main explanations for losses of plant diversity (Vitousek et al. 1997, Bobbink et al. 1998, Sala et al. 2000, Grime 2002, Tilman et al. 2002, Stevens et al. 2004, Suding et al. 2005, Tamis et al. 2005). Or in the words of Silvertown (2005): ‘Sold as the farmer’s friend, in an age of increasing atmospheric pollution, artificial fertilizers are fast becoming the enemy of diversity.’ According to Grime’s (1973, 2001) ‘hump-backed’ model of the relation between species richness and productivity, there is a peak in species richness at intermediate productivity, and above this productivity level species richness declines rapidly because only a few fast-growing species are successful in the competition for light.

Habitat fragmentation

Human interference has strongly affected the configuration of natural and semi-natural habitats and increased the degree of habitat fragmentation, in the Netherlands (Weeda 2000-2005, Fig. 1.5) as well on a global scale (Vitousek et al. 1997, Hassan et al. 2005). As a result of habitat deterioration and fragmentation, fewer, smaller and more isolated habitat patches harbour correspondingly fewer, smaller and more isolated plant populations, which are more vulnerable to influences from adjacent areas.

Habitat fragmentation is regarded as one of the major causes of global biodiversity loss (Vitousek et al. 1997, Millennium Ecosystem Assessment 2005), and encompasses at least three different components (Hanski 1998, 2005, Opdam et al. 2003, Honnay et al. 2005). The first and most direct component is the pure loss of habitat, which leads to local extinctions (Hassan et al. 2005). The second component, reduction of the size of habitat patches, leads to smaller populations which have a higher risk of local extinction. This higher extinction risk of small populations is caused by their greater sensitivity to environmental, genetic and demographic stochasticity (Shaffer 1981, Gilpin & Soulé 1986, Pimm et al. 1988, Nee & May 1997, Menges 2000, Booth & Grime 2003, Vergeer 2005, Mix 2006).

As a third component, increasing *spatial and temporal isolation* of habitat patches reduces both the *spatial connectivity* and the *temporal continuity* of habitats for a given species. This has serious consequences for metapopulation dynamics: isolated populations (both spatially and temporally) have lower chances to re-

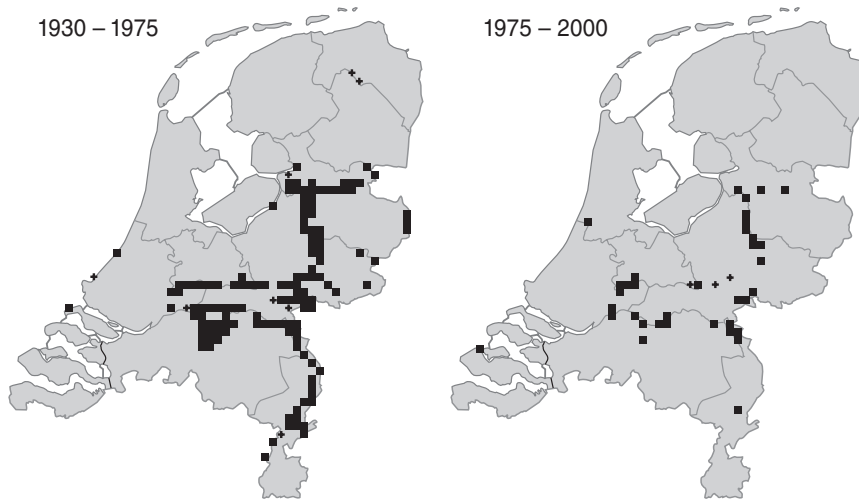


Figure 1.5: Example of habitat fragmentation: temporal changes in the distribution pattern of species-rich grasslands on river dunes (alliance *Sedo-Cerastion*). From Ozinga & Schaminée (2004), after data from Weeda et al. (2000–2005). Filled squares represent plots with descriptions of the species composition; + symbols represent observations without further descriptions.

colonize suitable sites that have become unoccupied (Hanski et al. 1996, Hanski & Ovaskainen 2000, Cook et al. 2005), thereby reducing gene flow between populations (Young et al. 1996, Ouborg et al. 1999, Ouborg & Eriksson 2004). An appropriate rate of seed dispersal can increase or maintain local species richness through colonization of suitable but as yet unoccupied sites, and through ‘*rescue effects*’, by which seeds from other sites sustain local populations that would otherwise become extinct (Levins 1969, Brown & Kodric-Brown 1977, Shmida & Ellner 1984, Pulliam 1988, Eriksson 1996, Hanski 1998, Loreau & Mouquet 1999, Keymer et al. 2000).

Changing dispersal processes

The transport of seeds between sites depends on external vectors. Several vectors are able to transport seeds between sites, including water, wind, birds and large mammals, each with their own characteristics. At the landscape level, these dispersal vectors act like a complex ‘*dispersal infrastructure*’. This dispersal infrastructure has changed dramatically in the Netherlands (see Chapter 8, Box 3) as well as in many parts of Europe and America (e.g. Ridley 1930, Salisbury 1961, Janzen 1984, Poschlod & Bonn 1998). Although such changes in dispersal infrastructure can be regarded as a large-scale ‘*natural experiment*’, the effects of changes in the availability of dispersal vectors on plant diversity has never been tested at large spatial and temporal scales, due to a lack of suitable data.

In conclusion, recent large-scale human interference has changed habitat quality, habitat configuration and dispersal infrastructure at an unprecedented rate. In contrast to the effects of changes in habitat quality, the effects of changes in habitat configuration and dispersal processes on the species composition of plant communities are poorly understood, and these are therefore the focus of this thesis.

Outline of the thesis

The aim of this thesis is to investigate the roles played by (1) niche-based processes, (2) dispersal processes and (3) abundance-based (trait-neutral) stochastic processes in the assembly of plant communities. The studies underlying the thesis focused on dispersal processes across various hierarchically related levels of organization (species, habitats, landscapes), in order to obtain more information on the relevance of dispersal traits for the spatial dynamics that we observe in the field. This will have resulted in specific predictions of the risks species run in fragmenting landscapes and on the possibilities for species-specific conservation measures.

The premise in this thesis is that differences in terms of relevant functional traits between species from local habitat patches and from the regional species pool can give clues to the processes at work in the assembly of local communities from regional species pools. The degree of over- or under-representation of certain attributes relative to random sampling implies the involvement of non-random processes. The remaining chapters in this thesis all relate to specific aspects of the assembly of plant communities and complement each other.

Chapter 2

This chapter offers a technical introduction on the classification of dispersal traits across large numbers of plant species.

LIMITATION OF SEED AVAILABILITY VERSUS ENVIRONMENTAL CONSTRAINTS

Chapter 3

The study reported in this chapter tested the hypothesis that the predictability of local plant species composition from environmental conditions is influenced by life-history traits related to mobility.

Chapter 4

This study tested the existence of a trade-off between local aboveground persistence and the ability for dispersal in space and time, focusing on the extinction side of the dynamic equilibrium between colonization and extinction.

Chapter 5

The study tested the hypothesis that variation in dispersal traits across plant communities is related to the position of communities along major environmental gradients. This hypothesis was tested for (1) the distribution of dispersal vectors across plant communities and (2) the degree to which species within communities have the potential to use multiple dispersal vectors.

DISPERSAL TRAITS VERSUS STOCHASTIC DISPERSAL

Chapter 6

This chapter reports on a study testing the effects of (1) random dispersal (neutral null model), (2) species pool effects (neutral model with dispersal limitation) and (3) dispersal traits (interspecific differences in dispersal limitation) on the probability of being present in a local community, using a spatially explicit analysis for a single habitat type.

DISPERSAL PROBLEMS DUE TO HUMAN INTERFERENCE

Chapter 7

In this study we quantified the importance of long-distance seed dispersal for regional survival of plant species, using wind dispersal as an example. We did this by first relating the dispersal traits of plant species to seed dispersal kernels and then relating the kernels (median distance and 99-percentile dispersal distance) to the regional survival of the species.

Chapter 8

We tested the hypothesis that differences between species in population trends over the 20th century in Northwest Europe could be explained by interspecific differences in their modes of dispersal, in combination with known changes in the effectiveness of dispersal vectors, and compared the results with trait-neutral and niche-based alternative explanations.

SYNTHESIS

Chapters 9 and 10

The final chapters integrate the results and provide a synthesis of the role of dispersal in community assembly, from both a theoretical (Chapter 9) and an applied (Chapter 10) perspective.

Box 1: A new tool in the search for community assembly rules: ecoinformatics

Among scientific projects on the assembly of plant communities, there is a trade-off between realistic complexity and simplification (Grime 2001, Hobbs et al. 2006). Although experiments are a prerequisite for a detailed understanding of processes involved in community assembly, these experiments typically involve small spatial and temporal scales, which makes generalizations difficult. Moreover, the experimental designs are often too artificial to represent natural systems (Hobbs et al. 2006), and serious weaknesses have been identified in the design and interpretation of many experiments with synthesized community assemblages (e.g. Huston 1997, Grime 2002, Díaz et al. 2003, Lepš 2004). We cannot afford to postpone applying our knowledge until we know all the details, as this will never be the case (Theobald et al. 2000, Opdam et al. 2003). Generalizations across larger sets of species and ecosystems therefore require complementary approaches.

This thesis explores such a complementary, statistical approach, based on the premise that the combination of large ecological databases can generate clues to the processes at work in the assembly of plant communities which are valid at larger spatial and temporal scales (Brown & Maurer 1989, Díaz et al. 2004, Ozinga et al. 2005a,b, McGill et al. 2006). More specifically, this thesis makes use of a large database of the species composition of small plots on the one hand (species \times plot matrix) and a large database of functional traits on the other (species \times traits matrix). The integration of large ecological databases at different organizational levels and across spatial scales to reveal new information can be regarded as an example of the emerging field of 'ecological informatics' or 'ecoinformatics' for short (Kareiva 2001, Ozinga et al. 2004, 2005a, Recknagel 2006).

The advantage of focusing on functional traits instead of species is that it simplifies raising the scale level from species to communities (Shipley et al. 2006). Moreover, the information on rare species, which are normally excluded from analyses at the species level, can be retained (Ferrier & Guisan 2006). Although the present approach is based on large databases from the Netherlands, we expect that the general principles revealed by it will also be applicable in other parts of temperate Europe and North America.

As regards functional traits, we used the LEDA database, which contains information on traits for the Northwest European flora (Knevel et al. 2003, 2005, Kleyer et al. in prep., see Chapter 2 for dispersal traits). The data describing species occurrences in local communities are derived from *'The vegetation database of the Netherlands'* which is available on the internet through the expert system SynBioSys (Schaminée et al. 2007, see Box 2), which com-

prises over 400,000 specific descriptions of the species composition of small plots (representing local plant communities). It is currently the largest database of local plant species co-occurrence data worldwide. The database is based on a large 'space-time window' (plots have been recorded throughout the Netherlands over the period from 1930 to 2000) and covers the entire environmental 'niche space' in the Netherlands.

Large datasets at the community or landscape level are generally notoriously difficult to approach from a statistical point of view, due to the large number of interactions between variables and the large proportion of data that do not satisfy the distributional assumptions required by many statistical tests. Recent developments in multivariate statistics, however, provide new powerful tools for the analysis of plant communities (e.g. Chytrý et al. 2002, McCune & Grace 2002, Ter Braak & Šmilauer 2002, Lepš & Šmilauer 2003, Ozinga et al. 2005a, Hobbs et al. 2006, Recknagel 2006). This facilitates a shift from traditional significance testing based on P-values (i.e. is the effect detectable) towards assessing the relative support in the data for multiple hypotheses (i.e. their relative ecological importance).

Box 2: The position of Dutch plant communities within a habitat template

Recurrent patterns of co-occurring species form the basis of a formal hierarchical classification of plant assemblages into abstract community types (syntaxonomy) in which each community type (syntaxon) is defined by a characteristic species combination (Braun-Blanquet 1932, Tüxen 1937, Westhoff & Van der Maarel 1978). According to the niche-based view of the assembly of plant communities, these predictable spatial patterns in local species composition are the result of the sorting of species along environmental gradients.

This Box gives an overview of the positions of all plant community types in the Netherlands along the major environmental gradients, based on ordination techniques (see also Chapter 3 for an alternative approach based on individual plots). The classification into community types has the advantage that it allows a comprehensive overview of habitat types. Even if such vegetation classifications to some degree represent arbitrary divisions of a continuum, these abstractions can offer valuable ecological information for habitat management and spatial planning (Van Leeuwen 1966, Ellenberg 1988, Rodwell et al. 2002, Hunt et al. 2004, Van der Maarel 2005). Our ordinations were based on a species-community matrix of 1214 species and 226 community types, based on approx. 400,000 original plot descriptions (Schaminée et al. 1995-1999 and Weeda et al. 2000-2005). Each community type is a summary of all the plots that belong to that community type, based on the similarity between plots in terms of species composition (Schaminée et al. 1995-1999). Each cell within this matrix shows the percentage of plots in which the species was present within the relevant plant community (frequency). Rare species, occurring within a single community with a frequency of occurrence less than 1%, were deleted. The positioning of plant community types in the Netherlands along three major environmental gradients was based on Detrended Correspondence Analysis (DCA). The ordination axes were interpreted in terms of environmental gradients by adopting Ellenberg indicator values for moisture, nitrogen availability, pH / base saturation, light availability, temperature and salt tolerance (Ellenberg et al. 1992, see Chapter 3 for technical details and a discussion of the reliability of this procedure). The resulting ordination axes define a kind of multidimensional 'habitat template'.

The ordinations revealed close correlations ($r > 0.9$) between the positions of communities, based on their constituent species along the ordination axes, and the environmental variables. This indicates that the variation between the abstract community types can be largely explained in terms of environmental variables. However, it should be noted that the explained vari-

ance at the level of individual plots is much lower (see Chapter 3). Figure Box 2.1 presents an ordination diagram of all Dutch plant communities (including saline and aquatic environments). Within this figure, each point represents the centroid of a community type. The first axis in the figure shows a clear transition from aquatic plant communities to terrestrial communities. The second axis separates salt marshes and coastal dunes from the inland communities.

For inland terrestrial plant communities, which are the focus of this thesis (areas shaded in grey in Fig. Box 2.1), a further ordination yielded a highly negative correlation between the first ordination axis and soil moisture (fig 2.2A, $r = -0.86$), while the second DCA axis is correlated positively with nutrient availability ($r = 0.81$) and pH / base saturation ($r = 0.74$). Nutrient availability and base saturation show a high correlation ($r = 0.72$). The third DCA axis is negatively correlated with light availability ($r = -0.75$). Different successional stages which occupy comparable positions in the environmental niche space as defined by DCA axes 1 and 2 are clearly separated along DCA axis 3 (Fig. Box 2.2, panel A versus B).

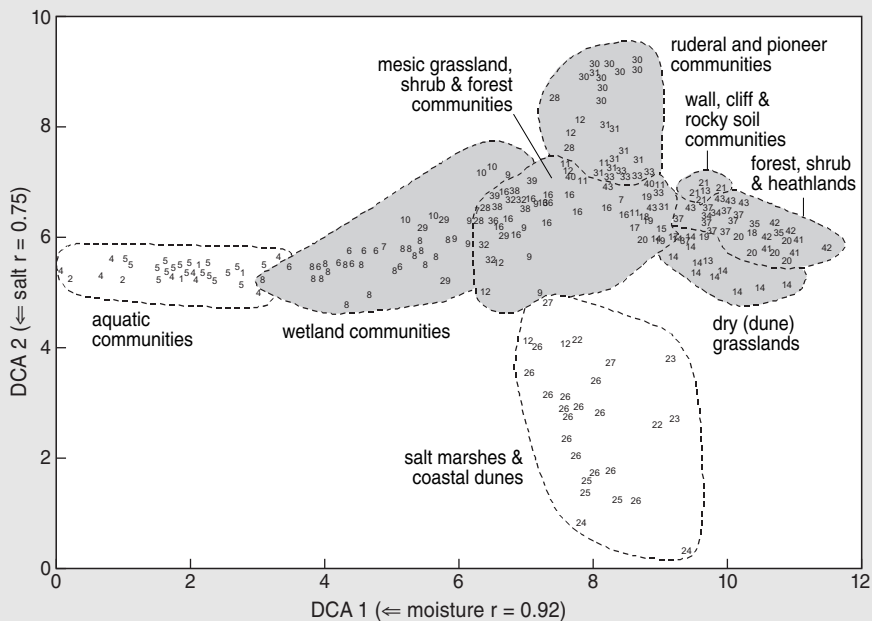


Figure Box 2.1: Position of all 226 Dutch plant communities within an ordination space showing DCA axis 1 (eigenvalue = 0.93) and DCA axis 2 (eigenvalue = 0.86). Numbers represent the centroids of syntaxonomic classes to which the communities belong (legend in Table 1). The areas shaded in grey were further analysed in the present study.

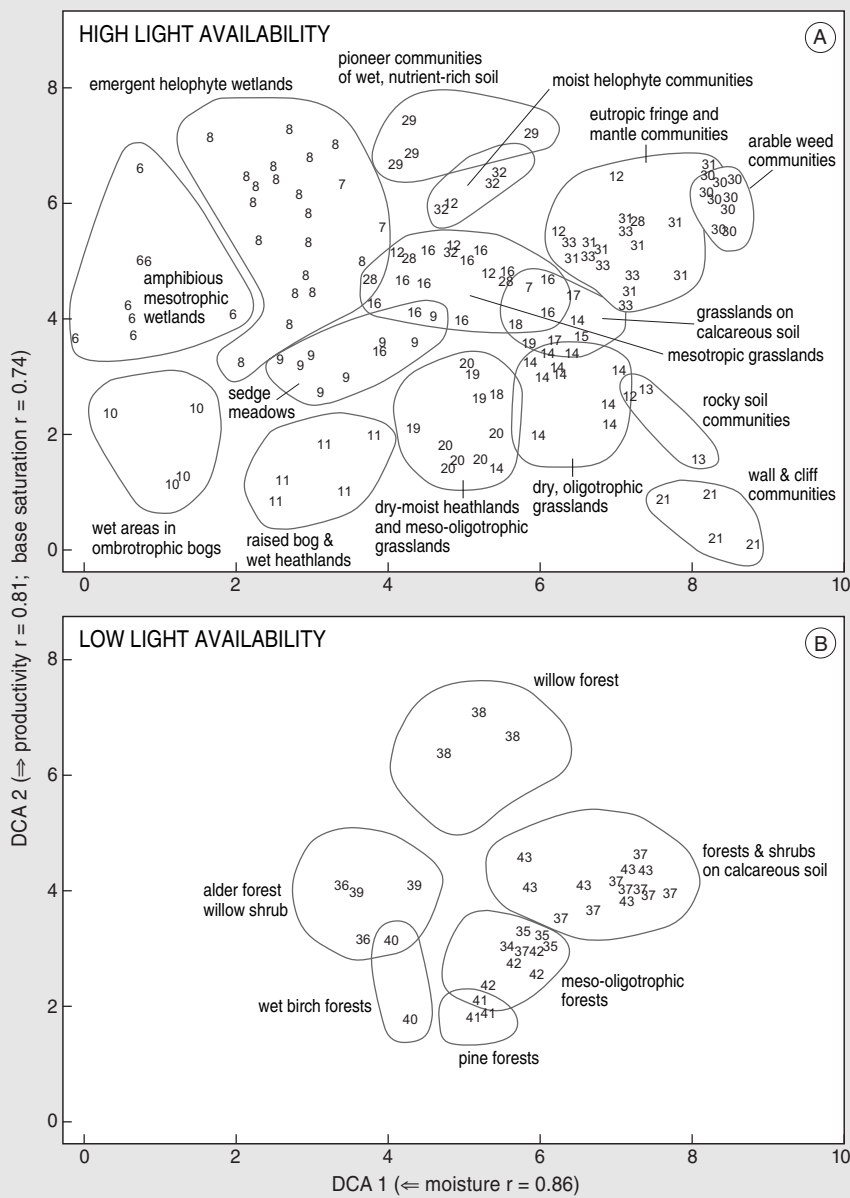
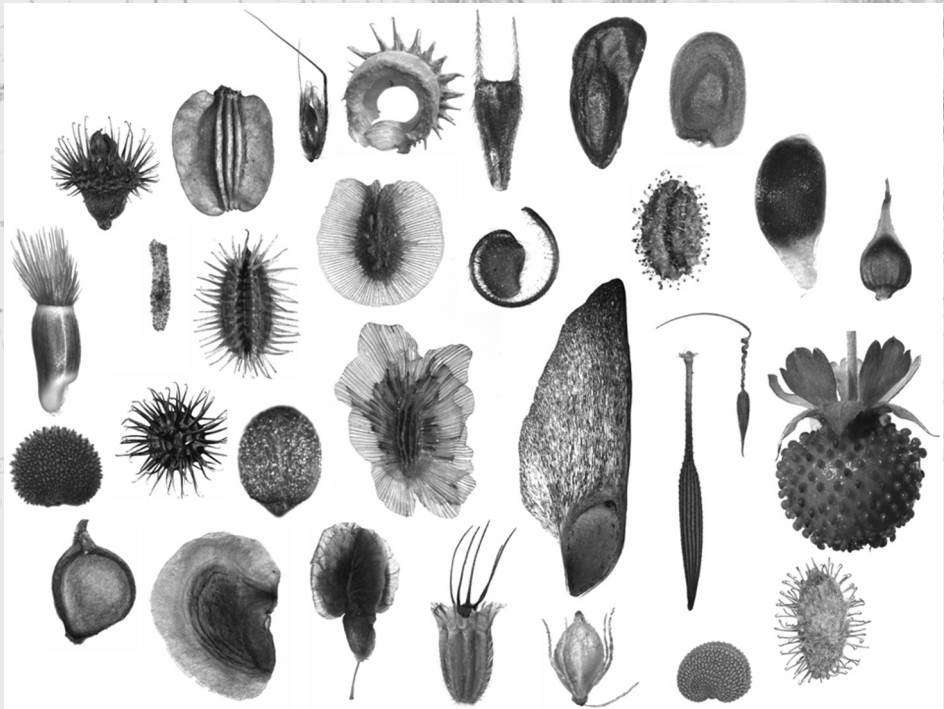


Figure Box 2.2: DCA ordination of the wetland and terrestrial plant communities showing the first two ordination axes, axis 1 (eigenvalue = 0.80) and axis 2 (eigenvalue = 0.69). Numbers represent the centroids of syntaxonomic class to which communities belong (legend in Table Box 2.1). Panel A: Communities dominated by non-woody species (score for DCA axis 3 < 4.5, corresponding to high light availability). Panel B: Communities dominated by trees and shrubs (score for DCA axis 3 > 4.5, corresponding to low light availability). N-communities = 170; N-species = 968.

Table Box 2.1: Description of inland terrestrial plant communities in the Netherlands, aggregated at the level of syntaxonomic classes according to Schaminée et al. (1995-1999) with brief descriptions. The number of associations assigned to each class is shown in parentheses.

Code	Community type	Characteristics
Wetlands and related communities on waterlogged soils		
06	<i>Littorelletea</i> (8)	Amphibious vegetation of oligo/mesotrophic soft waters
07	<i>Montio-Cardaminetea</i> (3)	Moss- and herb-rich vegetation of water springs
08	<i>Phragmitetea</i> (19)	Reed and sedge-dominated swamps
09	<i>Parvocaricetea</i> (8)	Transitional mires, fens
10	<i>Scheuchzerietea</i> (4)	Vegetations of bog hollows and moorland pools
11	<i>Oxycocco-Sphagnetes</i> (5)	Ombrogenic raised bogs
28	<i>Isoeto-Nanojuncetea</i> (4)	Dwarf amphibious vegetation on oligo-mesotrophic soils
Grasslands, fringe communities and heathlands		
12	<i>Plantaginetea majoris</i> (7)	Heavily trodden or inundated grasslands
13	<i>Sedo-Scleranthetea</i> (2)	Pioneer grasslands on nutrient-poor, stony soils
14	<i>Koelerio-Corynephoretea</i> (12)	Grasslands of dry, sandy, nutrient-poor soils
15	<i>Festuco-Brometea</i> (1)	Grasslands of calcareous soils
16	<i>Molinio-Arrhenatheretea</i> (12)	Nutrient-rich, mesic (pastures, hay meadows) grasslands
17	<i>Trifolio-Geranietea sanguinei</i> (2)	Fringe vegetation of woodlands on calcareous soils
18	<i>Melampyro-Holcetea mollis</i> (2)	Fringe vegetation of woodlands on poor soils
19	<i>Nardetea</i> (4)	Grasslands of rather moist, nutrient-poor soils
20	<i>Calluno-Ulicetea</i> (6)	Temperate heathlands on nutrient-poor soils
Synanthropic and chasmophytic vegetation		
21	<i>Asplenietea trichomanis</i> (4)	Vegetations of rock faces, fissures and ledges
29	<i>Bidentetea tripartitae</i> (4)	Ruderal comm. of nutrient-rich riparian habitats
30	<i>Stellarietea mediae</i> (9)	Annual, herb-rich ruderal and agrestal communities
31	<i>Artemisietea vulgaris</i> (9)	Perennial subxerophilous ruderal communities
32	<i>Convolvulo-Filipenduletea</i> (4)	Tall-forb communities on wet and nutrient-rich soils
33	<i>Galio-Urticetea</i> (6)	Nitrophilous communities of woodland and riparian fringes
34	<i>Epilobietea angustifolii</i> (1)	Tall herb-rich communities of woodland clearings and gaps
Woodlands and shrubs		
35	<i>Lonicero-Rubetea plicati</i> (3)	Bramble scrubs
36	<i>Franguletea</i> (2)	Willow scrubs
37	<i>Rhamno-Prunetea</i> (9)	Mantle communities of temperate deciduous woods
38	<i>Salicetea purpureae</i> (3)	Willow and poplar riparian woods and scrubs
39	<i>Alnetea glutinosae</i> (2)	Alder woodlands
40	<i>Vaccinio-Betuletea pubescentis</i> (2)	Birch woodlands
41	<i>Vaccinio-Piceetea</i> (3)	Pine woodlands and planted conifer woodlands
42	<i>Quercetea robori-petraeae</i> (4)	Deciduous temperate woodlands on nutrient-poor soil
43	<i>Querceto-Fagetea</i> (6)	Deciduous temperate woodlands on calcareous soil



Classification of dispersal traits of vascular plants

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S.M. Hennekens, J.H.J. Schaminée & J.M. Van Groenendael

Selection of propagule types (seeds and fruits) showing the high morphological diversity.
(seed photos from Cappers et al. 2006)

Abstract

Based on available data we compiled a database for the Dutch flora with aggregated data at the species level for (1) the ability for long-distance dispersal by five dispersal vectors, (2) the ability for dispersal by multiple dispersal vectors. The resulting species – trait matrix formed the basis for the analyses in other chapters. Raw data were extracted from the LEDA database (life-history traits of the Northwest European flora) and adapted to a classification with three ordinal classes. Dispersal abilities cannot be translated directly into a species specific probability for a given dispersal distance since this is highly context dependent. The actual transport of propagules by a given dispersal vector depends on landscape characteristics, climatic conditions, the numbers of seeds produced and properties of the local dispersal vectors. Since differences in dispersal attributes can be quantified more easily, we have adopted a trait-based approach as a proxy for dispersal potential. For each dispersal vector, the classification of dispersal abilities is given supplemented with information on properties of the dispersal vector in a landscape ecological context. The ability of species to be transported by multiple dispersal vectors ('polychory') appears to be the rule rather than the exception.

Introduction

It is increasingly acknowledged that local plant species richness and community composition is affected by both niche based processes and by dispersal processes (e.g. Huston 1994, Grace 1999, Tilman 1999, Grime 2001, Whittaker et al. 2001, Ozinga et al. 2005). Both sets of processes act as filters on the pool of regionally available species from which local communities are assembled. These filters operate on traits, rather than on taxa (Keddy 1992, Díaz et al. 1999, 2004, Grime 2001, Lavorel & Garnier 2002). Hence, in order to arrive at process-based nature conservation and nature restoration, we need information on functional traits for large sets of species. Moreover a focus on traits allows ecological predictions beyond the scale of local communities.

Three groups of traits are considered to be important for the spatial and temporal dynamics of plant species (Grubb 1977, Tilman 1994, Eriksson 1996, Ehrlén & Van Groenendael 1998, Cain et al. 2000, Grime 2001, Strykstra et al. 2002, Muller-Landau et al. 2003, Ozinga et al. 2005), namely: (1) potential for long-distance dispersal, (2) potential to build up a persistent soil seed bank ('dispersal in time'), and (3) adult persistence. We focus on the first group of traits, thus dispersal in space, since this information was not yet available in a comparative way.

Information on functional traits for dispersal is scarce and scattered (Weiher et al. 1999, Bakker et al. 2000, Bonn et al. 2000), but recently data for the North-west European flora have been made available through the internet in the LEDA database (Knevel et al. 2003, 2005, Stadler et al. 2006, Kleyer et al. in prep., www.leda-traitbase.org). Based on data from the LEDA database we compiled a species-trait matrix for the Dutch flora with aggregated data at the species level for the ability for long-distance dispersal by five dispersal vectors. Raw data were adapted to a classification with three ordinal classes. Based on the resulting species – trait matrix, the ability for dispersal by multiple dispersal vectors was quantified. The resulting species – trait matrix formed the basis for the analyses in other chapters.

Quantification of the ability for long-distance dispersal

In plants, in contrast to most animals, dispersal is mostly passive: Seeds or other *propagules* (dispersal units) are transported away from the parent plant by external '*dispersal vectors*' such as wind, water or animals (Ridley 1930, Van der Pijl 1982). The various vectors of dispersal differ in the efficiency and the spatial scale at which they transport propagules. We are mainly interested in propagule transport between patches by *long-distance dispersal* (>100m; cf. Cain et al. 2000), since metapopulation dynamics in fragmented landscapes are mainly determined at this spatial scale. We therefore only considered the following dispersal vectors, all providing highly efficient long-distance dispersal: water, wind, the fur of large

Table 2.1: Overview of the dispersal vectors with a high efficiency for long-distance dispersal (LDD) included in the database (Ridley 1930, Van der Pijl 1982, Müller-Schneider 1983, Bonn et al. 2000, Knevel et al. 2005).

Dispersal vector	Transport mechanism
Water (hydrochory s.s.)	propagules floating on water-surface
Wind (anemochory)	propagules with reduced falling velocity
Mammalian dung (endozoochory by mammals)	survival of the digestive tract of mammals
Mammalian fur (epizoochory by mammals)	adhesion of propagules to fur of mammals
Bird droppings (endozoochory by birds)	survival of the digestive tract of birds

mammals, the dung of large mammals and droppings of frugivorous birds (see Table 2.1). Humans as dispersal vectors were not taken into account, as this would involve various trait syndromes, and comparative data for large sets of species are lacking.

The efficiency of various dispersal vectors for the seed transport of a given species can be classified based either on differences in actually achieved dispersal distance or on differences in attributes that increase the capacity for long-distance dispersal by a given dispersal vector (Muller-Landau et al. 2003). Dispersal distances can be described by a ‘*dispersal kernel*’, which is a probability density function that describes seed arrival at distance x from the parent plant (Clark et al. 1998). The shape of the ‘tail of the dispersal kernel’ (i.e. long-distance dispersal) depends on rare events and is extremely difficult to quantify (Ouborg et al. 1999, Cain et al. 2000; Bullock & Clark 2000; Nathan & Muller-Landau 2000, Nathan et al. 2002). The probability of ending up in the tail of the dispersal kernel is not only dependent on traits of the species, but also on landscape characteristics, such as vegetation structure, presence of barriers and availability of dispersal vectors, and therefore case specific. Our ability to predict dispersal kernels in realistic landscapes is therefore still very poor (Clark et al. 1998, 2003, Nathan 2005, 2006, Nathan et al. 2005). There is for example a strong discrepancy between observed migration rates of forest herbs after glacial periods, which are in the order of magnitude of $100\text{--}1000 \text{ m/yr}$, and dispersal distances of up to 10 m/yr that were actually measured in the field (*Reid’s paradox*; Clark et al. 1998). Even perfect information on the dispersal distance of all seeds in a population would only provide a case-specific documentation of differences in actual dispersal distance (Clark et al. 1999, Tackenberg et al. 2003; Nathan et al. 2003, Nathan 2005). It is therefore not realistic to precisely quantify the probability of seeds dispersing over distances of $>100\text{m}$ for many species under various conditions for all dispersal vectors.

Since dispersal attributes can act as a proxy for dispersal ability and these can be quantified more easily (Weiher et al. 1999, Tackenberg 2001, Tackenberg et al. 2003, Pakeman et al. 2002, Boedeltje et al. 2003, Couvreur et al. 2004, Knevel et al. 2005, Römermann et al. 2005), we have adopted a *trait-based approach*.

The available data were aggregated by assigning each species to one out of three ordinal classes for each dispersal vector (Table 2.2). The classification provides us with species specific values that are independent of the spatial context and thus comparable across different areas and different habitats. Although this classification of the continuum is less precise for individual species, it allows generalizations at the level of large species pools. It is important to note that many species have high dispersal abilities for more than one long-distance dispersal vector (*polychory*). In most chapters of this thesis this classification was even further simplified by combining the lowest two classes leading to a binary classification (0/1).

Table 2.2: Potential for propagule transport by the dispersal vector under consideration. Further details on the classification are presented for the individual dispersal vectors.

Class	Dispersal ability
0	low, no attributes that facilitate dispersal over distances >100m
1	intermediate
2	high, attributes that facilitate dispersal over distances >100m

The classification of the dispersal ability for various dispersal vectors is based as far as possible on measurements of simple parameters ('soft traits' or '*indicator parameters*' cf. Hodgson et al. 1999, Weiher et al. 1999, Bonn et al. 2000, Tackenberg 2001, Knevel et al. 2005, Römermann 2006) that are relatively easy to quantify and that provide good correlates with 'hard traits' which may be more accurate, but which are problematic to measure for large sets of species (Hodgson et al. 1999, Weiher et al. 1999, Ouborg et al. 1999, Bonn et al. 2000, Lavorel & Garnier 2002, Cornelissen et al. 2003). For example, the fall velocity of propagules after a phase of acceleration is regarded as a reliable predictor of dispersal ability by wind (Sheldon & Burrows 1973, Askew et al. 1997, Tackenberg et al. 2003, Katul et al. 2005). Further details on each dispersal vectors are presented below. To underline the context specific nature of seed dispersal, the discussion of the classification of individual dispersal vectors is supplemented with some brief information on properties of the dispersal vector in a landscape ecological context.

Dispersal by water (Hydrochory)

Propagule traits

Morphological or physiological adaptations of propagules that increase the ability to float on the water surface (buoyancy) include: low specific weight (e.g. due to air filled structures such as spongy tissues, balloons or air-catching hairs or due to

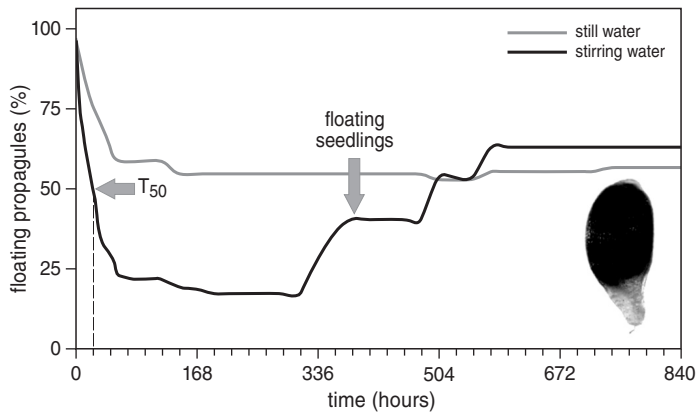


Figure 2.1: Example of the results of buoyancy experiments for the plant species *Luzula multiflora*. In this example the T_{50} value can be deduced from the results (indicated by the left arrow), but it is not possible to quantify the T_{10} value. In this experiment germinated seedlings started to float (indicated by the right arrow), indicating that seedlings can be dispersed over long distances. This figure also demonstrates differences in floating ability between still and stirred water.

large surfaces such as wings), water repellent seed or fruit coat, and high oil content (Praeger 1913, Ridley 1930, Baskin & Baskin 1998). In many grasses and sedges the bract remains attached to the seed as a ‘balloon’ and encloses a small amount of air.

For several species the dispersal capacity by water is mainly or solely dependent on *floating vegetative parts* (Ridley 1930, Feekes 1936, Boedeltje et al. 2003, 2007) or on *floating seedlings* (Ridley 1930, Huiskes et al. 1995, own observations; Fig. 2.1). For riparian plants, floating seedlings can be regarded as a quite elaborated dispersal strategy. Germination on the bottom promotes the establishment near the parent plant in favourable conditions, while under less favourable conditions (e.g. if the seedling cannot anchor itself by the radicle due to the hard soil or heavy wave action) the floating seedlings may disperse over considerable distances.

Properties of the dispersal vector

Whether water can act as an efficient dispersal vector not only depends on the floating ability of seeds but also on the landscape ecological context, e.g. the frequency and extent of inundations. Andersson et al. (2000) performed experiments with wooden cubes to mimic seed dispersal and deposition by boreal rivers. For free flowing rivers they found that species richness of the established vegetation increased with the number of deposited cubes. The dispersal kernel was in general leptokurtic with an increase of average and maximum dispersal distance with the size of the river (Andersson et al. 2000). The shape of the dispersal kernel,

is driven largely by landscape elements that trap propagules (e.g. curves or other obstacles along rivers; Schneider & Sharitz 1988, Nilsson et al. 1991, Johansson & Nilsson 1993, Andersson et al. 2000).

The relation between floating time and dispersal distance is strongly dependent on landscape characteristics. In fast flowing boreal and alpine rivers all species with floating seeds can be dispersed efficiently by water. In lowland rivers, regulated rivers or stagnant water bodies, in contrast, the proportion of seeds in drift traps relative to the abundance in the species pool is positively related with floating time (Jansson et al. 2000, Andersson et al. 2000, Nilsson et al. 2002, Boedeltje et al. 2003). This suggests that in regulated rivers, disrupted by dams, short-floating seeds do not float long enough to disperse successfully across impounded river sections.

Classification criteria for dispersal ability

Many species float well without clearly visible morphological adaptations (Praeger 1913, Johansson et al. 1996). Thus, classifications based on simple morphological traits tend to underestimate hydrochory. Measurements of the floating capacity can give a more accurate classification of the dispersal capacity by water. Our classification is based on studies in which the *floating time of propagules* is quantified (see Table 2.3 for criteria). This is expressed as the time after which 50, 10 and 0 % of the seeds still float (see Fig. 2.1 for an example). Ideally the estimation of the floating capacity should be determined in stirring water (Ecklund 1927, Feekes 1936, Danvind & Nilsson 1997, Bill et al 1999, Boedeltje et al. 2003). Experiments without stirring tend to overestimate the floating ability (e.g. Ecklund 1927, Feekes 1936). For the classification we also used data on viable seeds trapped in nets or in drift-line material. This information was used only for the classification if data on floating capacity were lacking. The dispersal ability for these species was classified as '1/2' because the exact floating capacity is not known. Given the stochasticity of peak floods (especially in rivers), drift sediments may contain additional rare species in comparison with field studies with nets. An important disadvantage of drift litter is that it might include wind dispersed propagules, and therefore species with only records from drift litter were not included in the classification. Seeds of several plant species can also be trans-

Table 2.3: Classification of the ability for long-distance dispersal by water.

Dispersal ability water	Criterion
0	propagules sink at once or float < 1 hour
1	propagules float 1 hour – 7 days
2	propagules float >7 days (including floating vegetative parts or seedlings)
1/2	propagules float > 1 hour, but floating capacity unknown

ported in the water column, but this dispersal mechanism is only effective in fast flowing rivers, and therefore this mechanism is not considered here. The database includes information on the ability to disperse by floating vegetative parts (0 or 1) or by floating seedlings (0 or 1).

Dispersal by wind (Anemochory)

Propagule traits

Plants can increase the efficiency for wind as a dispersal vector by decreasing the fall velocity of propagules and by increasing the height at which propagules are released. The constant rate of fall of propagules after a phase of acceleration (*terminal velocity*, V_{term}) is regarded as the most important indicator of dispersal ability by wind for a given species (Sheldon & Burrows 1973, Augspurger 1986, Green & Johnson 1989, 1996, Andersen 1992, Askew et al. 1997, Jongejans & Schippers 1999, Nathan et al. 2003, Tackenberg et al. 2003, Katul et al. 2005). Species with a low terminal velocity have a higher ability to profit from uplifting air turbulence which is important to give seeds access to airflow above the vegetation (Nathan et al. 2002, 2003, Tackenberg 2003, Soons et al. 2004, Katul et al. 2005).

In general V_{term} increases with *propagule weight* (Burrows 1975, Tackenberg 2001, 2003, Fig. 2.2). Seeds with a weight of less than about 0.01 mg ('dust seeds') are likely to be effectively dispersed by wind due to their small surface area relative to their weight (Burrows 1975). Many other plant species have special appendices on the seeds that increase the surface-area relative to the seed weight, such as wings or pappus-like structures. For a given propagule weight, the possession of a pappus or a large wing, substantially lower the terminal velocity (Fig. 2.2). The degree to which these structures enhance the potential for dispersal by wind is dependent on the 'wing-loading', which is the propagule's weight over the surface of the wing / pappus (Burrows 1975, Sheldon & Burrows 1973, Dale 1989, Sipe & Linnerooth 1995, Minami & Azuma 2003).

In general seeds with a well developed *pappus* have a relatively low terminal velocity for a given propagule weight (Fig 2.2). Species with a higher terminal velocity than expected from propagule weight, are in general characterized by weakly developed pappus-like structures (e.g. *Galinsoga* spec. with a pappus of small scales). Seeds with *large wings* have a weaker between seed size and V_{term} . Here the a-central position of the centre of gravity relative to the wing is probably more important (Sipe & Linnerooth 1995, Minami & Azuma 2003). The possession of large asymmetric wings (samaras), which leads to auto-rotating propagules, appears to be very effective in reducing V_{term} for propagules that weigh over 5 mg (Fig. 2.2).

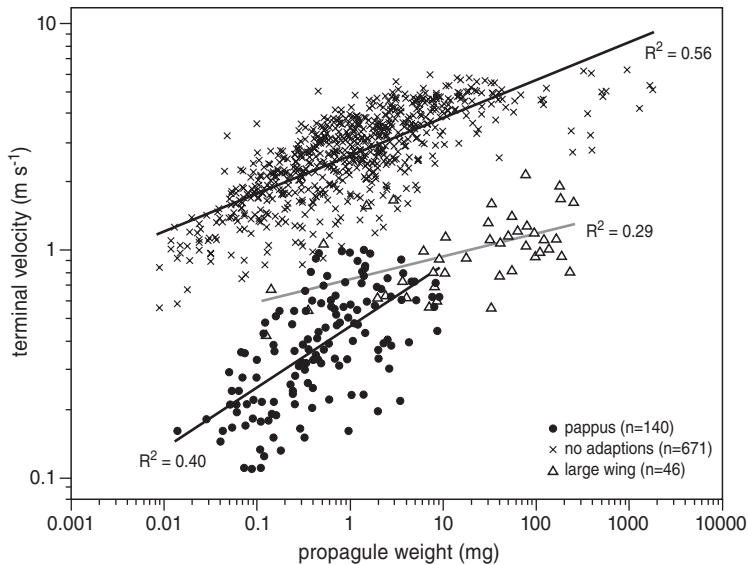


Figure 2.2: Relationships between propagule weight and terminal velocity plotted on logarithmic scales. Species are divided into three groups according to the presence of adaptations which reduce wing-loading: pappus-like structures, large wing-like structures or with no obvious structures.

Plant traits

Plants can also increase the potential for wind dispersal distance by increasing the *release height of the propagules* (Nathan et al. 2002, Tackenberg et al. 2003) but this parameter should be considered relative to the surrounding vegetation (Grace 1977, Oke 1987, Green & Johnson 1996, Soons & Heil 2002). The relatively high potential for wind dispersal observed in several tree species with winged propagules, can be attributed to the considerable release height (Green & Johnson 1996, Nathan et al. 2002, Tackenberg et al. 2003).

Properties of the dispersal vector

Most models on wind dispersal (e.g. Sharpe & Fields 1982, Andersen 1991) and wind tunnel experiments (e.g. Van Dorp et al. 1997, Strykstra et al. 1998) do not take into account vertical turbulence and can therefore lead to underestimation of the fraction of seeds dispersed over long distances. Adding vertical turbulence greatly increases model performance, because uplifting events, in which upward vertical wind velocity exceeds terminal velocity of seeds, is crucial in determining long-distance dispersal (Bullock & Clarke 2001, Nathan et al. 2002, Tackenberg 2003, Soons et al. 2004a, Katul et al. 2005, Nathan & Katul 2005). Tackenberg 2003 suggested that seed uplifting is mainly caused by thermic turbulence. In an unstable atmosphere (with low horizontal wind velocity and high surface heating),

thermic turbulence can lead to a net updraft, which can reach values of 3 m/s for several minutes above 20-100 m (Tackenberg 2003). Soons et al. (2004), however, argue that mechanically produced vertical turbulent air movements under high wind velocity conditions are more important for long-distance dispersal.

Dispersal of complete inflorescences or whole plants rolling on the ground surface and driven by wind ('tumbleweeds' or '*chamaechory*') can occur for plants with spherical growth forms (Ridley 1930, Feekes 1936). This way of wind-dispersal is only effective for long-distance dispersal if the vegetation cover is below 20% (Feekes 1936), e.g in open sand-dunes and along shorelines.

Classification criteria for dispersal ability

The classification of the ability for dispersal by wind adopted in this database is based on a combination of terminal velocity (V_{term}) and the mean height of seed release (H_{rel}). The criteria for the three classes in Table 2.4 are based on the results of model simulations by Tackenberg (2001, 2003). This mechanistic model simulates the proportion of propagules exceeding a reference distance under various landscape topographies and weather conditions. We used the results of model simulations with a reference distance of 100 m with standard weather conditions for central-European grasslands (Tackenberg 2003). For species with low dispersal abilities for wind, the proportion of propagules exceeding 100 m was < 0.008 , for the intermediate category the proportion was 0.008-0.064, and for species with a high ability for wind dispersal the proportion of long-distance transport was > 0.064 . These proportions are very sensitive to weather conditions, but the relative ranking of species is rather stable (Tackenberg et al. 2003), allowing a relative classification at the species level. For species without data on terminal velocity, this parameter was estimated from the propagule weight and the presence of morphological structures which increase wing-loading (pappus or wing, see Fig. 2.2).

Table 2.4: Classification of the ability for long-distance dispersal by wind. The classification is based on a combination of release height of the propagules (H_{rel} in m) and the falling velocity of propagules after a phase of acceleration (terminal velocity, V_{term} in m/s). The criteria are based on the results of model simulations by Tackenberg et al. (2003). Values in the cells give the terminal velocity for a given release height.

Dispersal ability wind	H_{rel}				
	0.2	1.0	2.0	5.0	10.0
0	>1.6	>1.8	>2.2	>2.6	>3.1
1	0.5-1.6	0.6-1.8	0.75-2.2	1.0-2.6	1.4-3.1
2	<0.5	<0.6	<0.75	<1.0	<1.4

Dispersal by mammalian dung (Endozoochory by mammals)

Propagule traits

The ability to be dispersed through dung of mammals (endozoochory) is dependent on (1) the *capacity to survive passage through the digestive tract* (propagule trait), and (2) the *probability to be eaten* (plant trait). The probability of propagules to survive passage through the digestive tract is suggested by several authors to increase with decreasing seed size and with decreasing variance in seed shape. Thus small and spherical seeds on average are more likely to be dispersed through endozoochory. Evidence for this generalization has been published for sheep (Özer 1979, Russi et al. 1992, Peco et al. 2006), cattle (Gardener et al. 1993), horses (Cosyns 2004), rabbits (Pakeman et al. 1999, 2002), red deer, roe deer and fallow deer (Heinken et al. 2002, Mouissie 2004) and hare (Heinken et al. 2002). The inverse relation between seed size and gut survival might be explained partly by a lower susceptibility to damage by chewing and a shorter retention time in the digestive tract for small seeds (Janzen 1982, Gardener et al. 1993, Blackshaw & Rode 1991, Pakeman et al. 2002, Mouissie et al. 2005). This dependence on seed weight and shape can also explain the high correlation with the capacity to form a persistent soil seed bank as shown by Pakeman et al. (1998, 2002), and Cosyns (2004). Evolution to maximize either gut survival or seedbank survival may have preadapted species for the other process (Pakeman et al. 2002). Seed weight and shape have thus a predictive power for the gut-survival ability. The high ability for dispersal through dung in small seeded seeds might be explained partly by a numerical effect (i.e. through the seed size – seed number trade-off) rather than by a seed-size effect per se as has been suggested by Eriksson & Jakobsson (1999) and Bruun & Poschlod (2006).

Another way of increasing the rate of gut survival is the occurrence of a hard seed coat or physical dormancy (Russi et al. 1992, Gardener et al. 1993, Miller 1995, Baskin & Baskin 1998, Peco et al. 2006). Several species with physical dormancy show even an increased germination after passage through digestive tracts, for example *Amaranthus*, *Chenopodium*, *Polygonum* and several *Leguminosae* (Ridley 1930, Müller-Schneider 1983, Russi et al. 1992, Ghassali et al. 1998). This is probably the result of increased permeability of the seed coat due to abrasion or due to removal of soluble inhibitors (Baskin & Baskin 1998).

Plant traits

A first condition that needs to be fulfilled for endozoochory by mammals is to increase its probability to be eaten through possession of a high forage quality of propagules or of the plants as a whole. Plant species differ largely in their foliage quality for herbivores, which is determined by the contents of nutrients, cellwall-components (e.g. hemicellulose, cellulose, and lignin) and toxic secondary metabolites (Klapp et al. 1953, Coley et al. 1985, Davidson 1993, Reich et al.

1999). Seeds of several toxic species can potentially survive passage through the digestive system, but are not eaten because they are poisonous and bitter. This has for example been shown for *Agrostemma githago* (Kempinski 1906). Janzen (1984) suggests that many small-seeded herbaceous plants are dispersed accidentally by large herbivores because the green parts have a high food quality so the foliage functions ecologically as an attractive fruit ('foliage is the fruit hypothesis'), although this seems not to be a general rule (Collins & Uno 1985). It is interesting to note that for most species, except a few dominants, the food quality of the single species will constitute only a small fraction to the meal of large mammalian herbivores (bulk feeders), and therefore not the food quality of a single species, but the food quality of the vegetation as a whole is of ecological relevance. Therefore, palatable plant species as a group might be regarded as a 'key-stone resource', whose fluctuating abundances are likely to influence grazing pressure (Davidson 1993). This mediates a positive interaction between plant traits and the behaviour of the dispersal vector, with herbivores sowing their own meal. On the other hand unpalatable plant species with mechanical or chemical defences may provide protection to palatable plant species ('associational resistance', Huntley 1991, Olff et al. 1999) and can prevent premature seed consumption of these species.

Properties of the dispersal vector

While the potential of species to be dispersed by mammalian dung depends on seed and plant traits, the actual probability for dispersal is also dependent on herbivore characteristics and the landscape ecological context. Differences in species composition in dung from various herbivores, foraging in the same area were shown by various authors, e.g. Janzen 1982, Welch 1985, Malo & Suárez 1995a,b, Heinken et al. 2002 and Cosyns 2004. Herbivore species differ in their home range, digestive system, food retention time, diet with regard to food quality and habitat preference. Herbivorous species can be classified according to their diet and digestive system in a continuum ranging from browsers to grazers (Hofmann 1989, Bodmer 1990, Clauss et al. 2003, Pérez-Barbería 2004). According to Clauss et al. (2003) the content of the stomach of grazers shows a distinct stratification in which denser particles sink to the bottom. The absence of stomach contents stratification in browsers is, in the view of Clauss et al. (2003), the best explanation for the less selective particle retention and generally shorter retention time in browsers than in grazers. In addition, there are important differences between animals that process their food in their hindgut (e.g. horses) and forestomach processors (ruminants such as deer, sheep, cattle). Ruminants are less able than hindgut processors to move large particles through their digestive system. Hindgut processors such as horses digest their food less thoroughly and defecate a higher proportion of large seeds (Stevens & Hume 1995).

Further differences between mammalian species can be explained by the relation between body mass and the spatial scale and precision of foraging (Ritchie &

Olf 1999). In general herbivores become less selective for certain plant species as body size increases (Demment & Van Soest 1985, Ritchie & Olf 1999). This implies that the forage of large herbivores has in general a higher proportion of seeds from plants with a low foliage quality. With regard to dispersal distance there are again pronounced differences between mammalian species, with a log-linear relation between body weight and maximum dispersal distance (Sutherland et al. 2000). Together the differences between mammalian species will translate in differences in spectrum of species which are dispersed through the dung of various herbivorous species.

Herbivory is not only important for the dispersal of seeds per se, but also for the establishment of seedlings by the creation of gaps through trampling (Grubb 1977, Bakker 1989, Bullock et al. 1995). Cosyns (2004) showed that cattle or horse dung in itself does not provide optimal germination conditions for most plant species and that effects of dung deposition were most pronounced in disturbed (sod-cut) plots. Malo et al. (1995) provide evidence that plant species that are efficiently dispersed through the digestive tract of mammals have in general an improved efficiency in the colonization of gaps generated by herbivores. This directed dispersal yields a higher probability of survival to maturity on a per seed basis (Wenny 2001).

Classification criteria for dispersal ability

The classification of the ability of species to be effectively dispersed by survival of the digestive tract of mammals is less straightforward, as compared to other dispersal vectors due to the lack of simple measurable morphological seed traits. Conventional classifications, based on simple morphological traits, tend therefore to underestimate the proportion of species with the ability to be effectively dispersed through survival of the digestive tract. Many species which are classified as 'unspecialised' in such conventional classification systems (e.g. Willson et al. 1990, Hughes et al. 1994, Hodgson et al. 1995) have been shown to be efficiently dispersed by large mammalian herbivores after gut passage survival (e.g. Janzen 1984, Müller-Schneider 1986, Malo & Suarez 1995a,b, Pakeman et al. 1998, 1999, Cosyns 2004).

Species were classified as endozoochorous if they fulfil two conditions: (1) they have been shown to survive the digestive tract of large mammals (two classes: 0/1), and (2) the propagules are frequently eaten under natural conditions (three classes: 0/1/2). The aggregated data are based on a multiplication of both fields (three classes). Emphasis is put on mammals with a medium to large home range, and separate fields are included for cattle, horse, sheep / goat, deer, pig and rabbit / hare. Most information is derived from studies on seedling germination from freshly collected dung (see Table 2.5).

There are at least two possible sources of bias in the classifications of the ability for dispersal by mammalian dung. Studies in which the abundance of germinating seeds was not quantified relative to the availability of seeds in the surrounding

Table 2.5: Classification of the ability for long-distance dispersal by mammalian dung.

Dispersal ability dung (mammals)	Criterion
0	not eaten by animals and/or no germination after passing the digestive tract
1	survival of seeds after passing the digestive tract low (at least 3 germinating seeds, but relative abundance in dung lower than 5% of relative abundance in the diet) and/or eaten rarely (plants with physical or chemical herbivore-defence)
2	survival of seeds after passing the digestive tract high (at least 3 germinating seeds and relative abundance in dung higher than 5% of relative abundance in the diet) <u>or</u> with physical dormancy and frequently eaten
1/2	seeds can survive digestive tract, but no further classification possible

vegetation are sensitive to a ‘sampling effect’, because abundant species have just by their high abundance a higher chance to be recorded. A second source of bias may stem from the inclusion of field data. Seedlings observed in dung in the field may have originated from wind dispersal, and therefore field data are less reliable. These less reliable data sources were only taken into consideration if no other information was available and those data were labelled with a question mark.

Dispersal by bird droppings (Endozoochory by birds)

Propagule traits

Although seed dispersal by bird droppings (‘ornithochory’) is a special case of endozoochory, it differs in some important aspects, both with regard to propagule traits and with regard to properties of the dispersal vector. Therefore dispersal by bird droppings is treated here separately. Plant species which can be dispersed through the digestive tract of birds can be divided into two broad groups: (1) species in which the seeds are surrounded by a fleshy, coloured, nutrient- and sugar-rich pulp, providing rewards to birds, and (2) species without nutritious reward. We focus on the former group.

In temperate regions, in contrast to tropical regions, plant species with fleshy fruits are mainly dispersed by frugivorous birds, and form only a small fraction of the diet of large mammals (Skeate 1987, Herrera 1987, 1995, Snow & Snow 1988, Jordano 2000). Plant species with fleshy fruits are in general relatively effectively dispersed by frugivorous animals due to high removal rates, and high survival-rates of the digestive tract (Herrera 1987, Snow & Snow 1988, Jordano

2000, Kollmann 2000). During fall bird migration in the Northern Hemisphere, plant species with lipid-rich fruits are the most highly preferred species (Stiles 1992). In several plant species the unripe fruits are prevented from premature consumption by defensive secondary metabolites (e.g. *Arum*, *Solanum*, *Lycium*, *Phytolacca*, *Rhamnus*, *Sorbus*). Furthermore, fruits from nearly all bird-dispersed plant species change colour on ripening from green to red or black (Stebbins 1971, Van der Pijl 1982, Herrera 1995). Wahaj et al. (1998) provide experimental evidence that secondary metabolites in fruit pulp influence retention time in bird guts, mediating a trade-off between dispersal distance (longer retention time) and seed viability (shorter retention time).

Many plant species without fleshy fruits have also been shown to be dispersed over long distances by birds, but the efficiency of birds as dispersal mode for most of these species is probably lower because the seeds are less selectively eaten and the mean survival rate is lower (e.g. Eikelboom 1941, Van der Pijl 1982). Based on an extensive literature review Ridley (1930) already states that it is probable that granivorous birds disperse many more seeds than is commonly thought. Salisbury (1961) assumed therefore that most seeds within a certain range of size at one time or another will be dispersed by birds, and Wilkinson (1997) suggests that for many wind dispersed seeds the wind dispersal mechanism is mainly adapted to local dispersal (over distances of a few canopy diameters) and larger scale dispersal is due to birds. The germination of some species is augmented by passage of their seeds through the digestive tract of birds, as has been shown for *Anthemis arvensis*, *Chenopodium album*, *Plantago lanceolata*, and *Sparganium emersum* (Salisbury 1961, Figuerola & Green 2002, Pollux et al. 2005). This may partly involve mechanic or chemical breaking of seed dormancy (Proctor 1968, Baskin & Baskin 1998). Another way in which seed passage in the digestive tract may increase seedling performance is by inhibition of fungal infections as has been shown by Eikelboom (1941).

Properties of the dispersal vector

In comparison to mammals, frugivorous bird species possess on average a higher forage and habitat selectivity (Herrera 1987, 1995, Snow & Snow 1988, Stiles 1992, Jordano 2000), and a higher degree of directed transport towards suitable safe sites for germination (Stiles 1992, Debussche & Isenbussche 1994, Wenny 2001). Moreover, the daily dispersal distances during migration are in general longer as compared to mammals (Sutherland et al. 2000). Migrating birds are capable of dispersing seeds over distances over hundreds of kilometres (e.g. Proctor 1968, Fridriksson 1975, Wilkinson 1997). Throughput times for seed defecation are usually in the range of 0.3-1.5 h (Snow & Snow 1988, Worthington 1989).

It is important to distinguish between seed-dispersers and seed-predators. This distinction is gradual and depends on the plant species involved. As a rule of thumb the following birds act as important seed dispersers in NW-Europe: Waterfowl (*Anatidae*), Thrushes (*Turdus* spp.), Crows, Jays, and Magpies (*Corvidae*),

some Warblers (e.g. Blackcap - *Sylvia atricapilla*) and Waxwing (*Bombycilla garrulus*). Several other bird-families, such as Grouses (*Tetraonidae*), Pheasants and Partridges (*Phasianidae*) and Doves (*Columbidae*) are only effective dispersers for plant species with relatively hard seeds and predators for other plant species. Sparrows (*Passeridae*), Tits (*Paridae*), Finches (*Fringillidae*) and Buntings (*Emberizidae*) can in many cases be regarded as seed predators or pulp-predators (Cramp et al. 1977-1994, Levey 1987, Snow & Snow 1988, Stiles 1992, Chang et al. 2005). Fleshy fruits of some plant species are only eaten by specialists. The bitter tasting fruits of *Viburnum opulus* for example are hardly eaten, with Waxwings (*Bombycilla garrulus*) as one of the exceptions. Periodic invasions of Waxwings therefore may be an important dispersal vector for this shrub species.

Classification criteria for dispersal ability

The classification is based on a combination of observations on wild or captive birds and propagule morphology (see Table 2.6). We define fleshy fruits as those propagules with soft, pulpy, nutrient- and sugar-rich layers around the seed(s). Some arillate seeds are included in this ecological definition, despite the differences in morphological derivation, because the function of an edible aril as a reward for dispersers is the same as that of an edible exocarp or pericarp (Van der Pijl 1972, Willson et al. 1989).

Table 2.6: Classification of the ability for long-distance dispersal by bird droppings.

Dispersal ability birds	Criterion
0	not eaten by birds and/or no germination after passing the digestive tract
1	germinating seeds after passing the digestive tract and not with morphological adaptations to attract birds
2	germinating seeds after passing the digestive tract high (at least 3 germinating seeds and relative abundance in droppings higher than 5% of relative abundance in the diet) and morphological adaptations to attract birds (fleshy fruit)
2?	morphological adaptations to attract birds (fleshy fruit), but no actual observations

Dispersal by mammalian fur (Epizoochory by mammals)

Propagule traits

In comparison to dispersal through the digestive tract of mammals, the potential for dispersal by adhesion in the fur of mammals (epizoochory or exozoochory) can be inferred more easily from propagule morphology. Various experiments have revealed that propagules with awns or burrs have on average a higher capacity to become attached and to remain attached on the fur of large mammals than seeds without such appendages (Carlquist 1981, Shmida & Ellner 1983, Sorensen 1986, Kiviniemi 1996, Kiviniemi & Eriksson 1999, Fischer et al. 1996, Heinken 2000, Gorb & Gorb 2002, Couvreur et al. 2004, 2005, Mouissie et al. 2005, Römermann et al. 2005). Moreover, seeds with hooked appendages have a longer median dispersal distance in fur of large mammals than smoother seeds (Willson 1993, Kiviniemi 1996, Kiviniemi & Eriksson 1999, but see Fischer et al. 1996). Although small, smooth propagules may also be dispersed in the fur of mammals (e.g. Shmida & Ellner 1983, Fischer et al. 1996, Heinken 2000) the capacity to become and to remain attached for a given seed weight is lower (Couvreur et al. 2004, 2005, Römermann et al. 2005).

Another attribute which might increase the attachment capacity is the excretion of a thin layer of sticky substances under moist conditions (mucilaginous seeds). The sticky layer, however, may primarily serve the purpose of cementing the seed to moist soil before germinating, restricting transpiration and increasing protection against pathogens (Ridley 1930, Baskin & Baskin 1998). In dry sites the seeds may be blown along the soil till they reach a spot sufficiently moist to exude the sticky layer and germinate. A further adaptation that probably facilitates external dispersal by mammals is the development of shedding-tolerant seeds or fruits to prevent premature seed release (Müller-Schneider 1983, Oba et al., 2000).

Comparative data on attachment capacity at the species level are scarce, since many field studies do not control for confounding factors such as vegetation structure, availability of propagules and animal behaviour. The potential for adhesive dispersal is driven by two key processes: 1) the ability of propagules to become attached to the fur of mammals, i.e. the attachment potential, and 2) the ability of attached seeds to remain attached, i.e. the retention potential (Fischer et al. 1996, Couvreur et al. 2004, Mouissie et al. 2005, Römermann et al. 2005, Will et al. 2007).

Plant traits

The proportion of propagules which becomes attached to fur is constrained by the height at which the seeds are released. The vast majority of species for which the propagules have frequently been observed in the fur of large mammals, have a seed release height between 0.2 and 2.0m (Sorensen 1986, Fischer et al. 1996, Graae 2002, Mouissie et al. 2005).

Properties of the dispersal vector

Among the large mammals, seeds in general show the best attachment and retention to the dense and fatty wool of sheep and to the long hairs of several Cattle breeds (e.g. Galloway-cattle, Scottish Highland cattle) and to a lesser extent to the long bristly hairs of Wild boar, while the sleek hairs of horses, short-haired cattle breeds (e.g. Holstein), rabbits and deer on average contain far less seeds (Ridley 1930, Mrotzek et al. 1999, Heinken & Raudnitschka 2002, Couvreur et al. 2004, Mouissie 2004). Sheep have been demonstrated experimentally to be able of transporting seeds over distances of more than 100 km (Manzano & Malo 2006). These distances largely exceed field observations on dispersal distances so far (Manzano & Malo 2006). Even within mammalian species there can be substantial differences in the suitability of the fur for seed attachment between breeds (W.A. Ozinga et al., unpubl. data for sheep breeds, Couvreur et al. 2004 for two cattle breeds).

The high efficiency of sheep for epizoochorous seed dispersal is further illustrated by the hundreds of plant species that have been reported in the wool of sheep. Until the beginning of the 20th century many alien plant species were introduced as so called 'wool aliens' in various centres for wool industry (e.g. Thellung 1912, Hayward & Druce 1919, Kloos 1939, Salisbury 1961). No less than 348 species of wool aliens were recorded by Hayward & Druce (1919) in a region with large quantities of sheep-wool import.

Not only interspecific differences in fur characteristics are important determinants of epizoochory, but also movement behaviour of mammals may influence

Table 2.7: Classification of the ability for long-distance dispersal by mammalian fur. Propagules may include calyx or other plant parts.

Dispersal ability fur	Criterion
0	<p>morphology: propagules with smooth surface <u>and not</u> with mucilagous; <u>or</u> when propagules with rough surface: release height < 0.2 or > 2m;</p> <p>field observations: species present in vegetation but not in fur or only in low quantities (<5% as compared to the relative abundance in the vegetation)</p>
1	<p>morphology: propagules with rough surface, but no hooks (raw hairs, pappus without barbs, style with little hook; <u>and</u> release height 0.2 - 2m;</p> <p>field observations: observed in fur in low quantities (> 3 seeds but relative abundance < 5% of relative abundance in vegetation)</p>
2	<p>morphology: propagules with awns, spiny teeth, burrs, pappus with barbs, style with barbs, hooked hairs or with excretion of viscid substances (mucilagous);</p> <p>field observations: observed in fur in high quantities (> 5% as compared to abundance in vegetation)</p>

both attachment and detachment of seeds (Bullock & Primack 1977, Fischer et al. 1996). For the detachment of seeds, grooming and wallowing are of particular importance (Agnew & Flux 1970, Sorensen 1986, Kiviniemi 1996). Furthermore the detachment may be facilitated by rain wash as has been observed for *Galium aparine* in sheep wool (W.A. Ozinga, unpubl. data).

Classification criteria for dispersal ability

The classification is based on two data types: (1) data on seed morphology and release height, and (2) data on observed attachment to the fur of mammals. Propagules with rough appendages (awns, hooks, bristles, including raw calyx) were classified as having a high potential for long-distance dispersal (Table 2.7). For the majority of species the two sources of data were consistent. In case of contrasting classifications we gave an expert judgement, labelled with a question mark. Emphasis is put on mammals with a medium to large home range, and separate fields are included for cattle, horse, sheep / goat, deer, pig and rabbit / hare. Within the LEDA project a standardized protocol was developed to quantify the species specific ability to remain attached to the fur of mammals (Römermann et al. 2005), while a protocol for the quantification of the ability to become attached was developed by Will et al. (2007).

Dispersal by multiple dispersal vectors (polychory)

Propagule traits

Many species have the potential to be effectively dispersed by more than one long-distance dispersal vector (Ridley 1930; Van der Pijl 1982; Higgins et al. 2003, Ozinga et al. 2004). These species can be regarded as generalists in terms of long-distance dispersal. On the other hand, several species have low potential for all five long-distance dispersal vectors (although many of them have special adaptations for short-distance dispersal, such as mechanisms to release seeds ballistically or nutrient-rich appendages to attract ants). For dispersal in general, potential dispersal by multiple vectors has been termed '*polychory*' (e.g. Ridley 1930; Van der Pijl 1982), but we restrict this term for the five long-distance dispersal vectors.

Classification criteria for polychory

The quantification of the potential use of multiple dispersal vectors is based on the number of long-distance dispersal vectors (out of five possible vectors) for which the species have a high dispersal ability.

Glossery

Trait: A well-defined, measurable property of the organism that is used comparatively across species. To be useful for analysis at the community or landscape level, traits should vary more between than within species (McGill et al. 2006). Species traits are assumed to represent evolutionary adaptations to their physical and biological environment (Ackerly 2003). Each species is thus characterized by a certain set of trait states (attributes).

A functional trait is one that strongly influences the performance of organisms (cf. McGill et al. 2006). A life-history trait is a trait that strongly influences population dynamics and mobility such as adult longevity, seed production and ability to disperse in space and time.

Propagule (=Diaspore): The actual dispersal unit, being any part of a plant (generative or vegetative) which can give rise to a new plant individual. Many seeds or fruits have special appendages to facilitate dispersal. These appendages include plumes and wings (wind dispersal), awns, spiny teeth or burrs (adhesion to animals), small oil rich appendages (elaiosomes facilitating ant dispersal) or fleshy pulp rich in simple sugars or lipids (vertebrate dispersal). The seeds plus the appendages are termed propagule and form the unit of dispersal. This definition includes vegetative parts, such as bulbs, rhizomes or stem fragments.

Vegetative dispersal: Several plant species have the ability to disperse by means of vegetative plant parts. Most, if not all, species can be made to regenerate from other plant parts than seeds, but we only regard plants which under natural conditions are capable of producing independent offspring by means of vegetative parts. Dispersal by vegetative parts is especially common in most aquatic and many riparian species (Titus & Hoover 1991, Grace 1993, Klimes & Klimesová 1999, Combroux et al. 2001, Andersson & Nilsson 2002, Boedeltje et al. 2003) and for this subset of species a trade-off with regenerative dispersal has been suggested (Boedeltje et al. 2007).

Dispersal vector: Mode by which propagules are transported.

Long-Distance Dispersal (LDD): Transport of propagules over distances >100m (cf. Cain et al. 2000) as necessarily to maintain meta-population networks of plants.

LDD vector: Mode of transport with a high (potential) efficiency to transport propagules over distances >100m (see Table 2.1).

Polychory: Capacity to use multiple dispersal vectors. In this paper indicated by the number of LDD vectors (see Ozinga et al. 2004).

Seed limitation: Community assembly is restricted by the low availability of seeds in suitable habitat patches (= seed-source limitation + dispersal limitation, see table 9.1). Seed limitation can be demonstrated experimentally by the establishment of a new population or an increase in population size when seeds are added (cf. Turnbull et al. 2000).

Seed-source limitation: Community assembly is restricted by the low abundance of populations in the surroundings that act as seed-sources (see table 9.1).

Dispersal limitation: Community assembly is restricted by the low rate of seed transport to suitable habitat patches (see table 9.1).

Main data sources

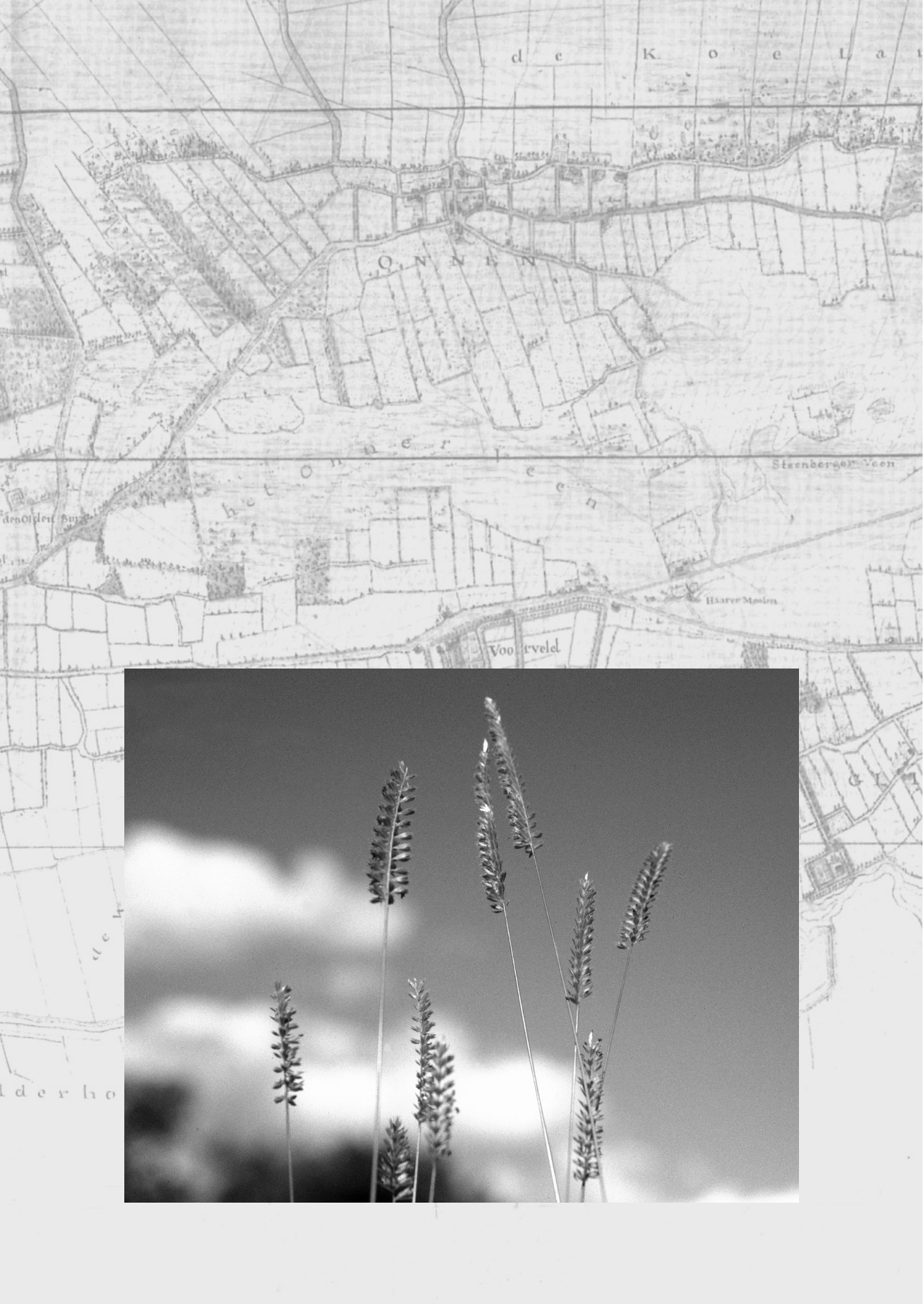
Dispersal by water: Andersson et al. 2000, Andersson & Nilsson 2002, Bakker 1989, Bill et al. 1999, Boedeltje et al. 2003, Bouwman et al. 2000, Cappers 1993, Danvind & Nilsson 1997, Ecklund 1927, Feekes 1936, Geertsema 2002, Guppy 1906, Heintze 1914, Huiskes et al. 1995, Katenhusen 2001, Koutstraal et al. 1987, LEDA traitbase (www.leda-traitbase.org), Martins 1857, Müller-Schneider 1986, Praeger 1913, W.A. Ozinga et al. (unpubl. data), Ridley 1930, Rommel 1938, Skoglund 1990, Van den Broek et al. 2005, R. Van Diggelen (unpubl. data), Van der Marel 1919, Vogt et al. 2004, Weeda 1985-1994, Wolters & Bakker 2002.

Dispersal by wind: Andersen 1992, 1993, Askew et al. 1997, Augspurger 1986, Bonn et al. 2000, Carlucci (unpubl. data), Feekes 1936, Greene & Johnson 1993, 1995, Hensen & Müller 1997, Jongejans & Schippers 1999, Jongejans & Telenius 2001, LEDA traitbase (www.leda-traitbase.org), Matlack 1987, Minami & Azuma 2003, Müller-Schneider 1986, W.A. Ozinga (unpubl. data), Ridley 1930, Schulz & al. 1990, Sheldon & Burrows 1973, Soons & Heil 2002, Tackenberg 2001, K. Thompson (unpubl. data), M. von Lampe (unpubl. data).

Dispersal by mammalian dung: Bakker 1989, Bakker & Olff 2003, Bonn et al. 2000, Bonn & Poschlod 1998, Bouwman et al. 2000, Campbell & Gibson 2001, Cosyns 2004, Dai 2000, Gardener et al. 1993, Ghassali et al. 1998, Heintze 1915, 1916, 1918, 1932, Heinken et al. 2001, Joenje 1978, Feekes 1936, Fischer et al. 1996, Knevel 1997, Knight & Walter 2003, Klapp et al. 1953, Klapp 1971, LEDA traitbase (www.leda-traitbase.org), Lennartz 1957, Malo & Suarez 1995a,b, Matějková et al. 2003, Meyers et al. 2004, Mouissie 2004, Müller-Schneider 1948, 1986, Özer 1979, Pakeman et al. 1999, 2002, Petrak 1987, Ridley 1930, Russi et al. 1992, Schmidt et al. 2004, Traba et al. 2003, Van Genderen et al. 1996, Weeda 1985-1994, Welch 1985.

Dispersal by bird droppings: Carrière & Van der Werf 1977, Cramp et al. 1977-1994, De Vries 1939, 1940, Eikelboom 1941, 1942, Heintze 1918, Herrera 1987, Joenje 1978, Johnson et al. 1985, Kempski 1906, Kollmann 2000, Krach 1959, Ridley 1930, Müller-Schneider 1986, Van der Pijl 1982, Van Genderen et al. 1996, Snow & Snow 1988, Van Steenis 1925, 1928, Weeda 1985-1994.

Dispersal by mammalian fur: Agnew & Flux 1970, Bonn et al. 2000, Bullock & Primack 1977, Couvreur et al. 2004, 2005, Fischer et al. 1996, Genard & Lescourret 1985, Graae 2002, Hayward & Druce 1919, Heintze 1918, Heinken 2000, Heinken & Raudnitschka 2002, Hillegers 1985, Joenje 1978, Mouissie et al. 2005, Mrotzek et al. 1999, Müller-Schneider 1986, Kiviniemi 1996, Kiviniemi & Telenius 1998, Kiviniemi & Eriksson 1999, Kloos 1939, LEDA traitbase (www.leda-traitbase.org), W.A. Ozinga (unpubl. observations on sheep; 1999-2002), Ridley 1930, Römermann et al. 2005, Salisbury 1961, Shmida & Ellner 1983, Schmidt et al. 2004, Stender et al. 1997, Thellung 1912, Weeda 1985-1994.



Predictability of plant community composition from environmental conditions is constrained by dispersal limitation

Ozinga, W.A., J.H.J. Schaminée, R.M. Bekker, S. Bonn, P. Poschlod, O. Tackenberg, J.P. Bakker & J.M. van Groenendael (2005).

Oikos 108: 555-561.

Species with a high capacity for long-distance dispersal have a higher ability to track the spatial and temporal dynamics of habitat patches as compared to immobile species. The latter group leaves many suitable habitat patches unoccupied. The propagules of Crested Dog's-tail (*Cynosurus cristatus*) can be effectively dispersed through attachment to the fur of large mammals.

Abstract

Despite recent modelling approaches integrating the effects of niche-based processes and dispersal-based processes on local plant species composition, their relative importance is still not clear. We test whether the predictability of local species composition from environmental conditions is influenced by dispersal traits. We analyzed a large database with co-occurrence data, using ordination techniques (DCA and CCA) to identify the major environmental determinants of species composition. The percentage of explained variance in occurrence was quantified for individual species with CCA. Effects of life-history traits on the predictability of occurrence patterns were tested by means of regression analysis, using a Generalized Linear Models approach. The results reveal close correlations between species composition and environmental conditions, implying that the predictability of the set of species that might occur in a given environmental setting ("habitat species pool") is high. The habitat species pool, however, reflects the potential species composition, and not the actual local situation. At the level of individual species, a large proportion (>90%) of the variation in occurrence remained unexplained. Predictability of species occurrence patterns was increased by a greater capacity for long-distance dispersal, greater adult longevity and the capacity to build a persistent seed bank. The results indicate that the predictability of species composition from environmental conditions is reduced by a few orders of magnitude by dispersal limitation and that poor dispersers are underrepresented.

Introduction

Understanding plant species diversity requires insight into the mechanisms that determine species richness, but also into the mechanisms that determine local species composition. Compared to species richness, species composition is more difficult to assess, as this requires a more detailed knowledge of the constituent species. Species composition involves not only the number of species and the abundance of each species, but also the specific nature of the species. Local species composition arises partly from stochastic processes such as local extinctions due to demographic drift and rare long-distance dispersal events, and partly from deterministic processes linking habitat characteristics to species-specific niches.

The prediction of spatial and temporal patterns of species composition can be approached by defining “community assembly rules” in terms of a set of “filters” which remove some of the species from the total species pool according to their functional attributes (Keddy 1992, Díaz et al. 1998). There are two major, complementary, views on the rules at work in structuring plant communities, each operating at a different scale level.

On a local scale, the so-called “niche assembly view” focuses on interactions between individuals of different species and, more specifically, on inter-specific niche differences. In this view, the species composition of a community is a deterministic consequence of physiological processes and biological interactions (e.g. Tilman 1985, Keddy 1992, Grace 1999). Patterns of species composition can then be largely explained by a few key environmental variables which act as filters on the available species pool.

On the other hand, the so-called “dispersal assembly view” focuses on larger scales both in space and time and assigns a more prominent role to stochastic events such as catastrophic changes in environmental conditions, local extinction and long-distance dispersal (e.g. Tilman 1994, Eriksson 1996, Zobel 1997, Clark et al. 1999). The dispersal assembly view was inspired by MacArthur and Wilson’s (1967) theory of island biogeography and by metapopulation theory (e.g. Levins 1969 and Hanski 1998). Metapopulation theory predicts that for a given plant species, only a fraction of suitable habitat patches are actually occupied, because species continually become extinct on a local scale ($<100\text{m}^2$) and the dispersal ability of most (if not all) species is expected to be limited, at least at larger spatial scales (Levins 1969, Eriksson 1996, Hanski 1998, Turnbull et al. 2000). Traits affecting species’ dispersal ability and local persistence can be expected to influence the dynamic equilibrium between colonisation and local extinction (Tilman 1994, Ehrén and Van Groenendael 1998, Eriksson 2000). This may translate at the community level into differences in local species composition between plots with the same environmental conditions (e.g. Tilman 1994 and Zobel 1997). Although the existence of interspecific differences in dispersal ability and local persistence is well established, this does not necessarily mean that these differ-

ences affect local species composition. When there is an interspecific trade-off among competitive ability and dispersal capacity (e.g. Tilman 1994, Ehrlén and Van Groenendael 1998), the net effect on local species composition may not be different from random sampling from the species pool (Hubbell 2001). The critical question is thus not whether dispersal is an important process, but whether differences in dispersal traits translate into differences in local species composition.

Most empirical studies of dispersal have focused on single plant species rather than on species assemblages. Only recently have modelling approaches started to integrate the effects of local and regional processes on local species composition (e.g. Tilman 1994, Chave et al. 2002, Mouquet and Loreau 2002, Leibold et al. 2004). It is still not clear, however, to what extent local species composition is determined by dispersal limitation. If local, niche-based, processes are the overriding factor determining local species composition, we expect no differences in predictability of occurrence between species that differ in their dispersal ability. Alternatively, if dispersal limitation is an important process, we expect that the correspondence between occurrence predicted on the basis of environmental conditions and the patterns that are actually observed in the field is smaller for species with limited dispersal ability. Such species will leave many suitable sites unoccupied. In other words: dispersal limitation will reduce our ability to predict local species composition from niche-based processes.

The degree of dispersal limitation for a species is influenced both by species traits and by landscape characteristics. At the landscape level, the degree of dispersal limitation can be affected by the abundance of species in the regional species pool and by the spatial configuration and connectivity of suitable habitats (Ouborg 1993, Zobel 1997, Hubbell 2001, Leibold et al. 2004). The present study focuses on the species level, and tests whether the predictability of local species composition from environmental conditions is influenced by life history traits. The study includes three life history traits that are considered to be important for the spatial and temporal dynamics of species (cf. Tilman 1994, Eriksson 1996, Ehrlén and Van Groenendael 1998, Muller-Landau et al. 2003), namely: (1) potential for long-distance dispersal, (2) adult persistence, and (3) potential to build up a persistent soil seed bank ("dispersal in time"). These three traits are expected to contribute positively to dispersal (that is, a high value for these traits reduces the degree of dispersal limitation) and hence positively to the predictability of the local occurrence of a particular species.

Recently extensive databases have become available on species composition and on species traits. Based on these databases we first quantify the major environmental variables that determine species composition. Then we test the hypothesis that the predictability of local species occurrence from environmental conditions reduces when dispersal ability is limited.

Methods

Dutch Vegetation Database

We used the vegetation database of the Netherlands, which comprises over 400,000 specific descriptions of the species composition of small plots (Hennekens and Schaminée 2001, see Box 2). It is currently the largest database of local plant species co-occurrence data worldwide. The database is based on a large “space-time window” (plots having been examined throughout the Netherlands over the period of 1930 to 2000) and covers the entire environmental “niche space” in the Netherlands. This provides the opportunity to explore relations between local species composition and environmental conditions at large spatial and temporal scales, based on vast numbers of data, an exercise best described as “ecoinformatics”. For computational reasons, we based our analysis on a selection of 22,770 plots out of the complete set. This selection was based on criteria with regard to plot size, representation of various environments, environmental homogeneity and prevention of spatial autocorrelation (see Schaminée et al. 1995-1999 for details). Plot size in this database has been scaled approximately according to the mean size of individual plants and ranges from 2x2 m (grasslands) to 10x10 m (forests). Plots located in saline and aquatic environments were excluded. For the 22,770 plots, the database includes information on the presence or absence of 1,492 species.

Identification of major environmental gradients

The relation between environmental conditions and species composition was determined by means of both indirect and direct ordination methods. Both approaches are complementary (Lepš & Šmilauer 2003). Indirect ordination methods provide a powerful tool to extract hypothetical environmental variables from species composition data (Hill and Gauch 1980, Peet et al. 1988, and Jongman et al. 1995). Analyses were performed using the CANOCO 4.5 program (Ter Braak and Šmilauer 2002). Since a unimodal response model is recommended for datasets covering large environmental gradients, as in our case, we focused on detrended correspondence analysis (DCA, Hill and Gauch 1980, Jongman et al. 1995). DCA constructs a theoretical variable (DCA axis 1) that best explains the variance in species composition between local communities, and constructs second and further axes with the constraint that they have to be uncorrelated with previous axes (Jongman et al. 1995). The relative positions of the plots along the axes provide a measure of their floristic similarity.

We interpreted the ordination axes in terms of environmental gradients by adopting Ellenberg indicator values for moisture, productivity (originally called nitrogen availability), pH / base saturation, light availability, temperature, and salt tolerance (Ellenberg et al. 1992). These indicator values are species-specific scores ranging from 1–9 (or 1–12 for moisture), which estimate the optimum occurrence of species along environmental gradients. Mean indicator values were

calculated for each plot, based on the species present in the community and these were correlated to the DCA axis scores for the plots. Evidence for the accuracy of these indicator values has been provided by several studies reporting a close correlation between average indicator values and corresponding measurements of environmental variables (e.g. Hill and Carey 1997, Schaffers and Šýkora 2000, and Diekmann 2003). It should be emphasized that the position of plots within the multidimensional ordination space is solely based on similarities in species composition. Ellenberg indicator values were only used indirectly to facilitate the interpretation of the ordination axes.

Predictability of species occurrence in relation to dispersal traits

We quantified the predictability of species occurrence from environmental conditions for individual species with the help of Canonical Correspondence Analysis (CCA; Ter Braak 1986, Palmer 1993, and McCune 1997). The CCA ordination was constrained by the same set of environmental indicator values as used in the unconstrained DCA ordination. These variables were entered in the CCA model by stepwise, forward selection. The statistical significance of each selected variable was tested for deviation from randomness by a Monte-Carlo permutation test. Residuals from the reduced model were permuted 499 times for each variable. The reduced model included the environmental variables that had already been selected, with the variable to be tested being excluded (Ter Braak and Šmilauer 2002). Strictly speaking, mean indicator values are no independent variables, since they are derived from the species composition, but the test of the significance of each environmental variable with CCA is just illustrative and the results are in accordance with the results from the indirect DCA ordination. The main aim of the CCA was the comparison of explained variance across species.

For each species, the goodness of fit of the CCA model was quantified as the cumulative fraction of the variance observed in the species occurrence data that could be explained by the fitted response curves in the CCA model, as calculated by the Cfit procedure within CANOCO 4.5. The goodness of fit for species *k* is quantified by this procedure as the regression sum of squares of the weighted regression of the data for species *k* on the ordination axes 1 to 4, expressed as a fraction of the total sum of squares for the species (Ter Braak and Šmilauer 2002).

The proportion of explained variance in species occurrences was linked to three traits, namely: (1) potential for long-distance dispersal, (2) adult persistence, (3) potential to build up a persistent soil seed bank (“dispersal in time”). We tested whether the predictability of occurrence from environmental conditions was influenced by these “mobility traits”. We used a simple binary classification in order to include as many species as possible, and to enhance comparisons between traits. Raw data were extracted from the LEDA database (Knevel et al. 2003, 2005, Kleyer et al. in prep.) and adapted to a binary classification (see Chapter 2). Species were classified as long-lived if their lifespan generally exceeds

two years. In terms of dispersal, a species was classified as having a high potential for long-distance dispersal (>100m, cf. Cain et al. 2000) if it can be effectively dispersed by wind, water or large mammals. The classification of seed longevity was based on Thompson et al. 1997. Seeds were regarded as persistent if their seed longevity index (cf. Bekker et al. 1998) exceeded 0.3. Only species which occurred in at least five plots and for which we had reliable trait data were selected for further analyses, while trees (often planted) were excluded, leaving a total of 593 vascular plant species.

Effects of traits on the predictability of species occurrence were tested by means of regression analysis, using a Generalized Linear Models procedure (GLM). Regression analyses were performed with the GenStat package (Lawes Agricultural Trust 2002). Because the response variable consisted of percentages, a logit link function was used, ensuring that the fitted values lay in the 0-100 range (Wedderburn 1974, McCullagh and Nelder 1989).

Results

The DCA ordination of the plots revealed close correlations between the position of plots along the DCA axes (based on species composition) and environmental variables indicated by Ellenberg indicator values (Table 3.1). This means that the differences in the position of plots within the ordination space can be explained largely in terms of these environmental variables. Moreover, the three ordination axes had high eigenvalues, implying a high resolution. The first ordination axis

Table 3.1: Summary of the DCA ordination. Number of plots: 22,770; number of species, including lichens and bryophytes: 1,492; number of occurrences: 433,564. The total inertia (sum of all unconstrained eigenvalues, representing the total amount of variance in the species data): 76.14.

Ordination axes	1	2	3	4
Eigenvalues	0.72	0.69	0.52	0.42
Lengths of gradient	9.594	9.307	8.441	9.285
Species-environment correlations:				
Total (multiple correlation)	0.973	0.923	0.917	0.86
Moisture	-0.93	0.28	0.17	-0.06
Productivity	-0.04	0.85	0.33	0.02
Light availability	0.23	-0.03	-0.78	0.07
Ph / Base saturation	0.18	0.73	0.04	0.28
Salinity	0.07	0.22	-0.54	0.10
Temperature	0.42	0.64	-0.11	0.13

was strongly negatively correlated with the mean moisture indication values ($r = -0.93$; Table 3.1), while the second DCA axis was positively correlated with productivity ($r = 0.85$) and pH / base saturation ($r = 0.73$). Productivity and base saturation showed a close correlation ($r = 0.72$, data not shown). The third DCA axis was negatively correlated with light availability ($r = -0.78$; Table 3.1).

The results of the CCA ordination were consistent with the results obtained by the DCA ordination. Monte-Carlo permutation tests showed that all environmental variables significantly contributed to the CCA model, but the highest explanatory values (as indicated by Lambda-A) were provided by moisture, productivity, and light availability (Table 3.2).

Despite the close correlation between the position of plots along the ordination axes and environmental variables, the proportion of explained variance in species occupancy patterns averaged only 7.7 (Fig. 3.1). The results of the regression analysis indicate that the degree of predictability of species occurrence from environmental conditions was significantly positively related to the ability for

Table 3.2: Test statistics for the environmental variables used in the CCA, based on Monte Carlo permutation tests. Variables were entered into the model with the forward selection procedure. Environmental variables are listed in order of the variance they explain. Lambda-A gives the additional variance explained by each variable as it was included in the model (variance explained by all variables: 3.51). All variables significantly contribute to the model ($P < 0.001$).

Variable	Lambda-A	F-ratio
Moisture	0.70	210.86
Productivity	0.63	191.18
Light availability	0.56	174.12
Ph / Base saturation	0.39	121.05
Salinity	0.27	83.64
Temperature	0.16	49.57

Table 3.3: Test statistics for the Generalized Linear Model, with the percentage of explained variance as the dependent variable and long-distance dispersal potential (LDD), adult longevity, seed longevity and their interactions as explanatory variables (d.f. total = 592; d.f. regression = 7). All interaction effects were not significant.

Parameter	F-ratio	P-value
LDD	179.90	<0.001
Adult longevity	37.66	<0.001
Seed longevity	5.22	0.023

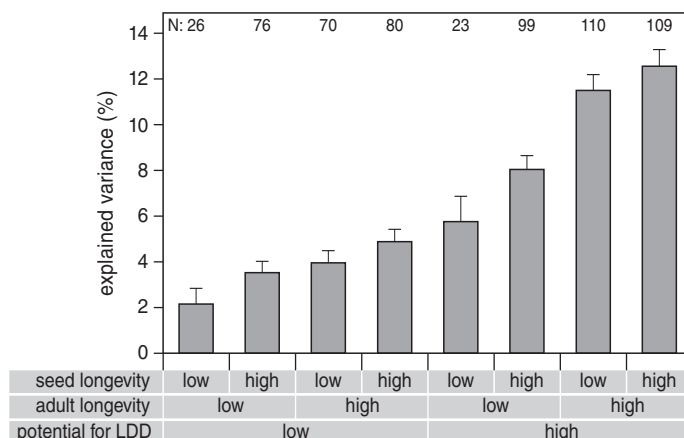


Figure 3.1: Percentage of variance in species occurrence as explained by the CCA model. Species were grouped into one of eight cells, according to their capacity for long-distance dispersal, adult longevity and seed longevity ($N_{\text{total}} = 593$; overall mean = 7.7).

long-distance dispersal and adult longevity, and to a smaller extent to the ability to build a persistent soil seed bank (Table 3.3). There were no significant interaction effects. The predictability of occurrence for species with low scores for all three traits was a factor 5.8 lower than that for species with a high score for all three traits (Fig. 3.1). The results imply that the predictability of local species composition from environmental conditions is reduced by dispersal limitation.

Discussion

The extensive databases used in the present study allowed us to quantify the effect of interspecific differences in dispersal traits on the predictability of species composition from environmental conditions. The results reveal close correlations between the position of plots along ordination axes and environmental conditions. The main environmental gradients reflect differences in the availability of (1) water, (2) limiting nutrients (highly correlated with pH), and (3) light (Tables 3.1 and 3.3). These environmental variables can be used as accurate predictors (“filters”) to assemble a list of species that are potentially able to coexist in a small-scale plot from a given habitat. In other words, the predictability of the “habitat species pool” (as a fuzzy set of species) on the basis of a given environmental setting was high. The habitat species pool, however, reflects the potential species composition for a given plot, rather than the actual local species composition. Many species which might be expected in a plot, given the combination of environmental conditions, are lacking. Unlike the high predictability of the *habitat species pool*, the predictability of the actual occurrence of individual species in

small-scale plots (and thus local species composition) was therefore relatively low (>90% unexplained variation).

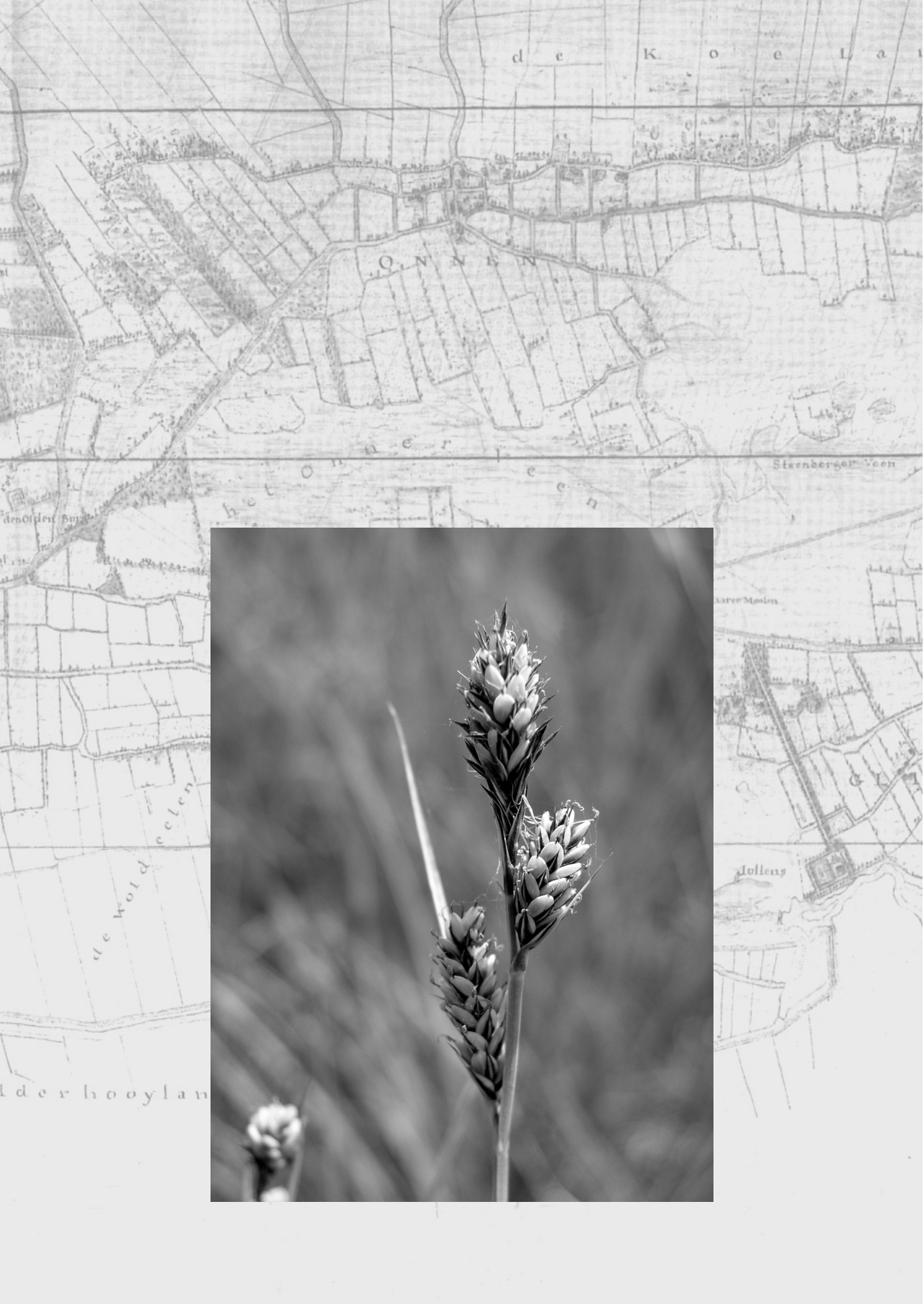
The large percentage of unexplained variance is a common finding in ordination models of plant communities (e.g. Økland 1999), and is usually explained by the notion that species data are often very “noisy” (Gauch 1982, Palmer 1993, Ter Braak and Šmilauer 2002) and that only a reduced number of explanatory variables is used (Ter Braak and Šmilauer 2002). The high proportion of unexplained variance is inherent in presence / absence data, since the probability of occurrence at specific sites translates into a binary pattern. Other factors reducing the predictability of local species composition from environmental gradients include small-scale ($<0.1\text{m}$) environmental heterogeneity (Tilman and Pacala 1993, Rosenzweig 1995) and inherent stochasticity in the location of individual plants (cf. Huisman and Weissing 1999). Alternatively, the low proportion of explained variance may indicate that local species composition is influenced by other processes, which were not covered by the ordination model. One of these additional mechanisms may be a “dispersal filter”. It follows from basic metapopulation theory (Levins 1969, Hanski 1998) that species occupy only a fraction of suitable habitat patches, because species continually become extinct on a local scale ($<100\text{m}^2$) and the dispersal ability of many species is expected to be limited at least at larger spatial scales. Within plots, there is thus a continuous turnover of species, as has been demonstrated by detailed field observations in grasslands by Van der Maarel and Sykes (1993). It is to be expected that dispersal limitation will reduce the correspondence between the predictions of species occurrence based on environmental conditions and actual field observations. Our results (Table 3.3) indicate that this was indeed the case. The degree of predictability of species occurrence from environmental conditions is significantly positively related to the ability for long-distance dispersal and adult longevity and to a smaller extent to the ability to build a persistent soil seedbank (Table 3.3 and Fig. 3.1). Apparently, the predictability of species composition is negatively affected by dispersal limitation. In brief, our results indicate that the large percentage of unexplained variance in species occurrence data was not just a matter of noise, but that the data may contain additional information about the degree of dispersal limitation of the various species. The present study does not take into account spatial aspects of dispersal, such as the degree of spatial and temporal isolation of plots relative to seed sources. A complementary study showed that when the spatial configuration of populations is taken into account, the predictability of species occurrence patterns can be further increased (Ozinga et al. 2005a; Chapter 6).

At first glance, there is a paradox between the high predictability of the composition of the habitat species pool and the low predictability of species composition on a small spatial and temporal scale. In our opinion, this apparent paradox can be resolved by recognizing the complementary nature of niche-based processes and dispersal-based processes on the assembly of community composition: The potential species composition (the habitat species pool as a fuzzy set of species) is

determined by physiological processes and interspecific interactions (environmental filters), whereas deviations from this potential composition are at least partly determined by the degree of dispersal limitation. We thus expect that the niche-based approach and the dispersal-based approach can reinforce each other.

Acknowledgements

This study was part of the Dutch Stimulation Program on Biodiversity and was funded by the Netherlands Science Foundation (NWO). We thank C.J.F. Ter Braak for technical advice on ordination methods, G.F.P. Martakis for statistical advice, S.M. Hennekens for technical assistance and R.K. Peet, A. Prinzing, C.J.F. ter Braak, E. van der Maarel and two anonymous reviewers for commenting on earlier versions of this manuscript, and J. Klerkx for language editing.



Local aboveground persistence of vascular plants: Life-history trade-offs and environmental constraints

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Journal of Vegetation Science 18: 489-497.

Buxbaum's Sedge (*Carex buxbaumii*) is an example of a species with a high local above-ground persistence and a very low dispersal ability. This sedge species is in Europe rare on the landscape scale (i.e. many unoccupied habitat patches), but in the few locations where it occurs it locally dominates the vegetation for many decades by clonal extension. The same phenomenon of local dominance by regionally rare species can also be observed for some other sedge species, like *C. aquatilis* and *C. hartmanii*.

Abstract

Questions: Which plant traits and habitat characteristics best explain local aboveground persistence of vascular plant species, and is there a trade-off between local aboveground persistence and the ability for seed dispersal and belowground persistence in the soil seed bank?

Locations: 845 long-term permanent plots in terrestrial habitats across the Netherlands.

Methods: We analysed the local aboveground persistence of vascular plants in permanent plots (monitored once a year during on average 16 years) with respect to functional traits and habitat preferences using survival statistics (Kaplan-Meijer analysis and Cox' regression). These methods account for censored data and are only rarely used in vegetation ecology.

Results: Local aboveground persistence is determined by both functional traits (especially the ability to form long-lived clonal connections) and habitat preferences (especially nutrient requirements). Aboveground persistence is negatively related to the ability for dispersal by wind and to the ability to accumulate a long-term persistent soil seed bank ('dispersal through time') and is positively related to the ability for dispersal by water.

Conclusions: The majority of species have a half-life expectation over 15 years (often much longer), which may contribute to time lags after changes in habitat quality or habitat configuration (the so called 'extinction debt'). The results provide evidence for a trade-off relationship between local aboveground persistence and belowground seed persistence, while the relationship with dispersal in space is vector specific. The rate of species turnover increases with productivity.

Introduction

Many empirical studies have shown that there is a continuous small-scale turnover of plant species (Watt 1947, 1960, Van der Maarel & Sykes 1993, Sykes et al. 1994, Herben et al. 1997, Klimeš 1999, Palmer & Rusch 2001), with the net result that plant species show temporal variation in their spatial distribution patterns as 'shifting clouds in the sky' (Grubb et al. 1982). This species turnover may be unidirectional (succession), cyclic (cyclic succession leading to shifting mosaics: Watt 1947, Remmert 1991, Olff et al. 1999) or non-directional. While the direction of vegetation changes (successional pathways) has received much attention this is less the case for the rate of vegetation change (Prach et al. 1993, Van der Maarel & Sykes 1993, Palmer & Rusch 2001). Van der Maarel & Sykes (1993) introduced the 'carousel model' to describe small-scale dynamics (cyclic or non-directional) within local plant communities in which species 'ride the carousel' at rates that may vary between species and between habitats. It is however not clear which factors determine the speed of the carousel (Van der Maarel & Sykes 1993, Palmer & Rusch 2001).

Vegetation dynamics are determined by a dynamic balance between colonization and local extinction (MacArthur & Wilson 1967, Huston 1994, Tilman 1994, Hanski 1998, Ehrlén & Van Groenendael 1998, Eriksson 2000, Palmer & Rusch 2001). In the present study we focus on the extinction side of this dynamic balance. At the scale of small plots the rate of local aboveground extinction can be expressed as the reciprocal of the mean or median time that a species persists in a plot ('residence time' according to Palmer & Rusch 2001, who defined residence time as the reciprocal of the probability of an occupied plot becoming empty per year). Here we define local aboveground disappearance as the disappearance of aboveground parts from year t to year $t+1$. For perennials belowground storage organs and seeds may persist, for annuals seeds could persist. Although local aboveground disappearance is correlated to local extinction it is thus not the same.

At the species level there may be intrinsic differences in the likelihood of local aboveground persistence (survival time), due to trade-offs between investments in attributes that enhance aboveground persistence and investments in other life-history traits. Adult lifespan is hypothesised to be negatively related to dispersal ability (Werner & Platt 1976, Grubb et al. 1982, Venable & Brown 1988, Tilman 1994, Ehrlén & Van Groenendael 1998, Eriksson 2000) and to seed longevity (Klinkhamer et al. 1987, Venable & Brown 1988, Rees 1993). This so called competition – colonization trade-off is generally explained by an underlying trade-off between seed size and seed number, where smaller-seeded species are superior colonizers and larger-seeded species are superior competitors, at least during the seedling phase (Venable & Brown 1988, Shipley & Dion 1992, Jakobsson & Eriksson 2000, Westoby et al. 2002). The advantage of large seeds, however, might not come through higher competitive ability, but rather through increased

tolerance of environmental hazards (Coomes & Grubb 2003, Turnbull et al. 2005). At the landscape scale species may ensure regional persistence by a high ability to colonize unoccupied sites or by reducing their risk of local extinction (MacArthur & Wilson 1967, Venable & Brown 1988, Tilman 1994, Hanski 1998, Eriksson 2000, Grime 2001, García & Zamora 2003). Local aboveground persistence and dispersal in space or through time may therefore be regarded as alternative strategies for regional persistence. Empirical evidence for such trade-offs between local aboveground persistence and dispersal ability, however, is very scarce and appears to be contradictory (Rees 1996, Thompson et al. 2002, Coomes & Grubb 2003, Moles & Westoby 2004, Kneitel & Chase 2004, Fenner & Thompson 2005). This might be explained, at least partly, by methodological difficulties in measuring local aboveground persistence (see below).

If there is a trade-off between aboveground persistence and dispersal ability, we may also expect a relationship between aboveground survival patterns and habitat requirements, since environmental constraints may impose restrictions to the viable trait combinations in a given habitat (Tilman 1990, Grime 2001, Kneitel & Chase 2004). The balance between traits enhancing local aboveground persistence and traits favouring dispersal in space or through time might depend on ecosystem properties such as disturbance regime (i.e. removal of aboveground biomass) and availability of resources (Huston 1994, Grime 2001, Westoby et al. 2002). The local aboveground persistence of a plant species may therefore also depend on its habitat preference.

Comparative data on the local aboveground persistence of plant species across habitats are sparse and generally from studies based on few populations of a limited number of species (Menges 2000, Palmer & Rusch 2001, Ehrén & Lehtilä 2002, Zens & Peart 2003). This is probably explained by at least two methodological problems. In the first place it is difficult to distinguish plant individuals within local communities (Ehrén & Lehtilä 2002), especially for perennial plants with capacities for clonal extension, where genetic individuals (genets) can split into spatially separated units (ramets). It is therefore very difficult to quantify the aboveground persistence of individuals, but from a metacommunity perspective the local performance of a subpopulation is more important than the longevity of an individual. Therefore, we focus on the local aboveground persistence of species (irrespective of the number of individuals) in a large set of permanent plots. A second methodological complication is the fact that for many time series an appearance or disappearance is not observed for many species. These incomplete data can be analysed with survival statistics (Zens & Peart 2003) to estimate local residence times of species. We used these survival statistics to analyse the effect of life-history traits and habitat requirements on local aboveground persistence and to test for existence of a trade-off between aboveground persistence and the ability for dispersal in space and time.

Methods

Analysis of local aboveground persistence with permanent plot data

Permanent plots can generate valuable insights in the temporal dynamic of plant communities (e.g. Dodd et al. 1995, Bakker et al. 1996, Foster & Tilman 2000, Silvertown et al. 2002). We used a selection of 845 permanent plots, distributed throughout the Netherlands and representing all major terrestrial habitats in the country. The plots have been recorded annually for at least 5 years up to 40 years and plot sizes range from 2 m × 2 m to 4 m × 4 m (roughly scaled according to the size of plant individuals). The selection was derived from a large survey of permanent plot data in the Netherlands (see Smits et al. 2002 for further details) and was based on availability of digital data, minimal observation period (>5 years), plot size and the absence of missing years in the time-series).

The permanent plots allow quantification of year-to-year local persistence of aboveground organs, but it should be emphasised that this is not the same as the persistence of genetic individuals. Three types of aboveground events can be distinguished in the transition between two subsequent years: 1) Local aboveground persistence (survival): a species stays present aboveground in both years; 2) aboveground appearance: a species is absent in one year and present in the next year; 3) local aboveground disappearance: a species disappears from a plot. At the species level we may quantify the residence time as the average time spent in a plot, as suggested by Palmer & Rusch (2001). Permanent plot data, however, contain many cases where the sample period does not include the full period of residence for a species. For a given species we often have both complete 'uncensored' data for which we know the exact period of local aboveground persistence (aboveground disappearance in the observation period) and incomplete 'censored' data for which the period of aboveground persistence is at least the observed period. For these data a simple regression analysis is inaccurate and may lead to wrong conclusions (e.g. Bressens et al. 1991, Zens & Peart 2003). Therefore we used statistical techniques (so-called 'survival statistics') that account for censored data: Kaplan-Meijer analysis and Cox' regression. The Kaplan-Meijer procedure and Cox' regression are based on estimating 'conditional' probabilities at each time interval and taking the product limit of those probabilities to estimate the survival rate (in our case: aboveground persistence) at each point in time (Hosmer & Lemeshow 1999). The probability is conditional because it refers only to those plants that survived to the interval under consideration. The permanent plots containing the species of interest are ranked according to increasing observed period of local aboveground persistence (survival time X in years). The estimation of the probability of the persistence (survival) at time t ($\hat{S}_{n(t)}$) can be obtained from equation 1 by cumulative multiplication.

$$\hat{S}_n(t) = \prod_1^n \left(1 - \frac{\delta_{n:i}}{n-i+1} \right) \quad (1)$$

Where:

S = estimate of probability of persistence (survival) at time t

n = ranknumber of time-series

δ = uncensored ($\delta=1$) or censored ($\delta=0$) time-series

i = rank number of the observed survival times

This function can be plotted stepwise for each time interval in a graph to obtain 'survival curves' and to estimate the survival time at the 75th, 50th and 25th percentiles. In order to extract the input parameters for the calculation of $\hat{S}_n(t)$ we have developed a computer routine to extract for every species X and $\delta_{n:i}$ for all the permanent plots in which the species occurs in at least one year.

All statistical analyses were performed with the software package SPSS 12 (© SPSS Inc. 1989-2003). For comparisons of survival curves between species groups (grouped according to functional traits, see below) the log-rank test within the Kaplan-Meier procedure was used. The Kaplan-Meier procedure is only suitable for analyses with at most one covariate with only a few levels. For the analyses of continuous variables and for the simultaneous analysis of several covariates we used Cox's regression model (or Cox's proportional hazards model) with stepwise selection of variables. As in logistic regression, the effect of one unit increase of a given variable adjusted for the other covariates is described by $e^{\beta i}$, the so-called hazard ratio. We used Wald statistics for significance testing (Hosmer & Lemeshow 1999).

We excluded species that occurred in less than 10 permanent plots and species that are frequently planted (i.e. many tree and shrub species), leaving a total of 276 species.

Classification of plant characteristics

Data on functional traits were extracted from the LEDA database of life-history traits of the Northwest European flora (Kleyer et al. in press, www.leda-trait-base.org) and adapted to a binary classification. We included three groups of traits that are considered to be important for the spatial and temporal dynamics of species (cf. Tilman 1994, Eriksson 2000 and Ehrlén & Van Groenendael 1998, Ozinga et al. 2005): (1) potential for long-distance dispersal, (2) potential to build up a persistent soil seed bank ('dispersal through time'), and (3) potential adult life-span and ability for clonal extension (see Table 4.1). By long-distance dispersal we mean dispersal over distances of roughly more than 100 metres (cf. Cain et al. 2000). We consider the following dispersal vectors with a high efficiency for long-distance dispersal: water (hydrochory), wind (anemochory), attachment to the fur of large mammals (epizoochory by mammals), and survival in the digestive tract of large mammals (endozoochory by mammals). In order to

Table 4.1: Overview of the functional plant traits used in the case study.

Plant characteristic	Description
Adult longevity	The potential life span of an individual adult plant (0 = annual or biennial, 1 = perennial)
Distance of lateral spread	Distance bridged by clonal spread (0 = ≤ 10 cm, 1 = > 10 cm)
Longevity of clonal connection	Longevity of the clonal parent-offspring connection (0 = transient, ≤ 1 year, 1 = persistent, > 1 year)
Dispersal potential water	Potential for Long Distance Dispersal by water (0 = low, 1 = high)
Dispersal potential wind	Potential for Long Distance Dispersal by wind (0 = low, 1 = high)
Dispersal potential fur	Potential for Long Distance Dispersal by fur of mammals (0 = low, 1 = high)
Dispersal potential dung	Potential for Long Distance Dispersal by dung of mammals (0 = low, 1 = high)
Seed longevity	Persistence in the soil seed bank (transient: < 1 year; short-term persistent: 1-5 years; long-term persistent: > 5 years)
Nutrient requirements	Ellenberg Indicator Value for nutrient (esp. nitrogen) requirements (1 = low, 9 = high)
base saturation	Ellenberg Indicator Value for base saturation of the soil (1 = low pH, 9 = high pH)
Moisture requirements	Ellenberg Indicator Value for moisture (1 = low, 9 = high)
Light requirements	Ellenberg Indicator Value for light requirements (1 = low, 9 = high)
Temperature requirements	Ellenberg Indicator Value for temperature (1 = low, 9 = high)

include as many species as possible and to facilitate comparisons between different dispersal vectors, we aggregated the available data into a binary classification for each vector, assigning each species a '1' if the species is effectively dispersed by a given vector and '0' if not (see Ozinga et al. 2004). For the classification of dispersal through time we used the seed longevity index (after Bekker et al. 1998), based on persistence data from the LEDA database (Thompson et al. 1997, Kleyer et al. in press, www.leda-traitbase.org): transient: index < 0.3 ; short-term persistent: index $\geq 0.3 - 0.5$; long-term persistent: index > 0.5 .

For clonal reproduction we classified the species according to the distance of lateral spread (≤ 10 cm or > 10 cm) and the longevity of the connection (≤ 1 year or > 1 year; cf. Klimeš et al. 1997, Van Groenendael et al. 1997).

The habitat requirements for individual species were based on Ellenberg indicator values for moisture, nitrogen availability, base saturation, light availability, and temperature (obtained from Ellenberg et al. 1992). These indicator values are species-specific scores ranging from 1-9 (or 1-12 for water), which estimate the optima for species along environmental gradients.

Results

There is a wide variation between species in their local aboveground persistence. Results of the Kaplan-Meier survival analysis for individual species, in Appendix 1, give times in years after which 75%, 50% and 25% of the plots are still occupied. Local aboveground persistence is, by necessity, strongly related to adult longevity (Table 4.2). The aboveground persistence among perennials is increased by the ability to form persistent (long-lived) clonal connections between parent and offspring ramets. It is, however, only the temporal aspect of the clonal connection which is of importance (longevity of the parent-offspring connection); the spatial aspect (distance of the parent-offspring connection / lateral spread) is insignificant.

Species with the ability to build up a long-term persistent soil seed bank have on average a lower aboveground persistence (Fig. 4.1). The same is true for species with a high potential for long-distance dispersal by wind. Species with a high potential for long-distance dispersal by water in contrast have on average a higher local aboveground persistence, while the effects of other dispersal vectors were not significant (Table 4.2).

With regard to habitat characteristics, local aboveground persistence decreases with increasing nutrient requirements (Fig. 4.1) and, to a much smaller extent, with increasing light requirements. Persistence increases with preferred base saturation of the soil (Table 4.2). This implies that the rate of species turnover is highest in communities with nutrient-rich soil conditions.

Table 4.2: Results of Cox' regression for hazard rate based on 276 species, 845 plots and 12,189 observed survival times (periods of local aboveground persistence) among which 27% were uncensored (aboveground disappearance in the observation period). For the significant variables that were included in the final multivariate model the following parameters are given: regression coefficient (β ; negative values indicate that the variable reduces the hazard rate and thus increases the local aboveground persistence, while positive values imply a trade-off), standard error (SE), the Wald test statistics (indication of the relative importance of the effect), and the significance of the regression coefficients β_i .

Variables	β	SE	Wald χ^2	Sig.
Adult life span	-0.601	0.044	182.46	<0.001
Longevity clonal connection	-0.358	0.045	64.37	<0.001
Nutrient requirements	0.213	0.030	49.29	<0.001
Dispersal potential wind	0.224	0.046	23.81	<0.001
Dispersal potential water	-0.190	0.040	22.27	<0.001
Seed longevity	0.085	0.022	15.23	<0.001
Base saturation	-0.120	0.035	12.12	<0.001
Light requirements	0.128	0.058	4.90	0.027

Discussion

Trade-off between aboveground and belowground persistence

Within the large group of perennial plant species, local aboveground persistence is strongly enhanced by the ability to form long-lived clonal connections between parent and offspring plants. These long-lived clonal connections may reduce local extinction risk due to the buffering effect against temporally suboptimal environmental conditions such as low resource availability or high disturbance intensity (Cook 1983, Oborny & Bartha 1995, Eriksson 1996, Eckert 2002). This buffering effect against local extinction is caused by the translocation of resources and photo-assimilates, which results in equalization of the environmental quality across space and time (Cook 1983, Oborny & Bartha 1995, Van Groenendael et al.

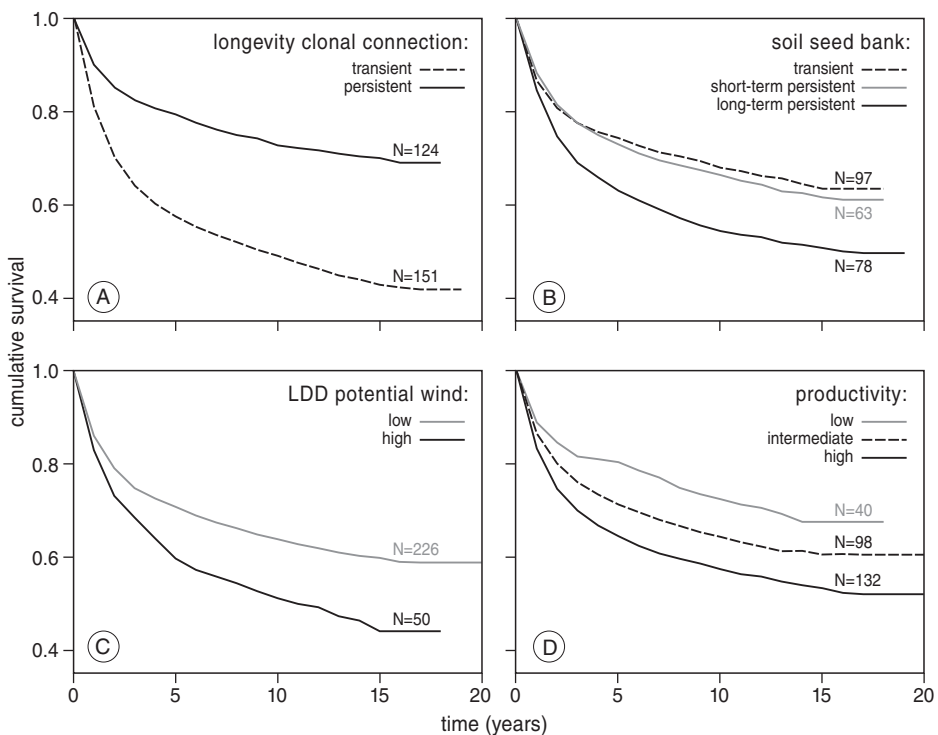


Figure 4.1: Aboveground local persistence illustrated with ‘survival curves’ related for various functional traits. The y-axis gives the cumulative percentage of plots in which the species persists at a given time. Species are classified according to functional traits or habitat characteristics. Panel A: Longevity of clonal connections between parent and offspring plant; Panel B: Ability to accumulate a persistent soil seed bank; Panel C: Ability for long-distance dispersal by wind; Panel D: Nutrient level at which the species has its highest frequency of occurrence. All curves within individual panels differ significantly ($p < 0.0001$), except in pane B where the curves for transient and short-term persistent seed banks are not significantly different ($p = 0.49$).

1996, Klimeš et al. 1997). The results suggest that it is the longevity of the clonal connection that is of importance for local aboveground persistence, while the spatial scale of clonal extension is insignificant.

At the landscape scale species may ensure regional persistence by a high ability to colonize unoccupied sites or by reducing their risk on local extinction (MacArthur & Wilson 1967, Venable & Brown 1988, Tilman 1994, Hanski 1998, Eriksson 2000, Grime 2001, García & Zamora 2003). Local aboveground persistence and dispersal in space or through time may therefore be regarded as alternative strategies for regional persistence. Our results demonstrate that plant species with the ability to build up a long-term persistent soil seed bank have on average a lower local aboveground persistence as compared to species with only short-term seed persistence in the soil seed bank (Fig. 4.1). This implies a trade-off relationship between aboveground adult persistence and belowground seed persistence, as suggested by Klinkhamer et al. (1987), Venable & Brown (1988) and Rees (1993). The trade-off relationship however appears to be rather loose and there are several species that combine a long-term persistent seed bank with a high local aboveground persistence (e.g. *Calluna vulgaris*, *Juncus acutiflorus*, *Ranunculus repens*; see Appendix). This loose relationship between regeneration traits might be explained by the fact that regeneration strategies do not necessarily reflect trade-offs in resource allocation, but may rather represent a spatio-temporal trade-off between 'an unsatisfactory present and the expectation for a brighter future at another place or at another time' (Southwood 1988, Strykstra et al. 2002).

With regard to dispersal in space, our results suggest that the hypothesized trade-off relationship with local aboveground persistence is less straightforward. Local aboveground persistence was indeed negatively related to the potential for dispersal by wind but was positively related to the potential for dispersal by water. This contrasting result might be explained by the complex relationship between seed mass (which is expected to be positively related to seedling survival in the competition – colonization trade-off) and dispersal ability. While the potential for long distance dispersal by wind is strongly related to seed mass (Augspurger & Franson 1987, Greene & Johnson 1993, Tackenberg et al. 2003, Soons et al. 2004), this is not the case for the potential for long distance dispersal by water (Praeger 1913). Moreover, many aquatic plants combine long-lived clonal connections with the ability for long-distance dispersal by stem fragments (Boedeltje et al. 2003). Apparently, dispersal ability cannot be regarded as a single trait (e.g. based on seed mass as in the competition-colonisation trade off), but should be differentiated according to dispersal vectors.

Species turnover increases with productivity

The results support the perspective that plant communities are dynamic entities, even on relatively short time scales (cf. Van der Maarel & Sykes 1993). Our results, however, indicate that local aboveground persistence decreases with in-

creasing nutrient requirements, and to a much smaller extent with increasing light requirements and preference for acid soils (i.e. persistence increases with base saturation of the soil). The positive relation between nutrient requirements and the rate of species turnover might be explained at least partly by differences in metabolic rates across productivity gradients. Evidence is accumulating that there is a fundamental trade-off between attributes enabling high rates of resource acquisition in productive habitats and attributes enabling efficient retention of resources in unproductive habitats (Grime et al. 1997, Díaz et al. 2004, Tjoelker et al. 2005). Relative growth rates and nutrient turnover tend to be larger for species characteristic of productive environments (Grime & Hunt 1975, Hunt & Cornelissen 1997, Meziane & Shipley 1999, Grime 2001). Within perennial species, high rates of resource acquisition and relative growth rate are inversely related to adult life-span (Stearns 1992, Enquist et al. 1999, Brown et al. 2004). The higher relative growth rate in productive habitats therefore is expected to lead to higher species turnover.

Comparable mechanisms might explain the decreasing local aboveground persistence with increasing light requirements, since high light requirements are generally associated with an on average shorter leaf lifespan (cf. Hubbell & Foster 1992, Westoby et al. 2002). In comparison to productivity, however, the relationship between light requirements and local aboveground persistence is relatively weak.

At the same time, habitats with a low nutrient and/or light availability may be less suitable for new colonists, probably due to the lower levels of resources left unused by the resident species for newly arriving colonists (Burke & Grime 1996, Davis et al. 2000, 2005, Foster & Dickson 2004, Tilman 2004). Therefore, these environments may select for longer local aboveground persistence. The environmental filtering in favour of species with attributes that increase local aboveground persistence might result in a lower species turnover in habitats with a low nutrient and light availability.

Local aboveground persistence and the extinction debt

For 55% of plant species included in our study the half-life residency expectation (once established) was over 15 years. Our results are in agreement with observations by various authors that many plants may persist in small plots for decades (e.g. Tamm 1956, Watkinson 1992, Økland 1995). Although competitive interactions are important in shaping plant communities (Huston 1994, Grime 2001, Tilman 2004), competitive exclusion is apparently often a very slow process for many species, especially in unproductive habitats, unless the environmental conditions suddenly change. Conservation biologists usually assume a causal relation between species distribution patterns and current habitat configuration. In metapopulations the frequency of occurrence is determined by the dynamic balance between colonization and local extinction. For species with a high local aboveground persistence, however, there will be a time lag between reduced seed

dispersal due to habitat fragmentation and the establishment of a new equilibrium in frequency of occurrence (Tilman et al. 1994, Eriksson 1996, 2000, Hanski & Ovaskainen 2002, Nagelkerke et al. 2002, Helm et al. 2006). For some species the current landscape may not support viable metapopulations anymore, resulting in regional extinction on the long-term. These doomed species with only remnant (cf. Eriksson 1996) populations may be regarded as ‘living deaths’ (cf. Diamond 1991) with present day distributions reflecting the configuration and land-use of past landscapes. Some authors therefore suggest that the present regional extinctions are only a forerunner of larger-scale future extinctions (‘extinction debt’ cf. Tilman et al. 1994). Our results suggest that time lags in local extinctions are most pronounced in habitats with a low nutrient availability. This implies that the extinction debt might be most severe in unproductive habitats and that species characteristic of these habitats might be most prone to underestimations of their extinction risk in changing landscapes.

Acknowledgements

This research was financially supported by the Netherlands Organization for Scientific Research (NWO-ALW), by the European Commission (LEDA-project, EVR1-CT-2002-40022) and by the European Science Foundation (05_EDIV_FP040-ASSEMBLE). LK was partly supported by grant no. 526/06/0723 of the Grant Agency of the Czech Republic. We kindly acknowledge Yzaak de Vries (University of Groningen) for help with collecting permanent plot data and Matthias Löwe (Radboud University Nijmegen), Dr. Patsy Haccou (University of Leiden) for statistical advices and Dr. Kerry Woods (Bennington College), Eddy van der Maarel (University of Groningen) and three anonymous referees for helpful comments.

Appendix 1: Results of the Kaplan-Meier survival analysis for individual species. Given are the times in years after which 75%, 50% and 25% of the plots are still occupied. For many persistent species it was only possible to give a minimum estimate for the 75 quartile because all observed periods of local aboveground persistence were censored (i.e. the actual local aboveground extinctions fell after the observation period). Nomenclature: Van der Meijden (1990).

Species name	Nplots	% Censored	T75	T50	T25
<i>Achillea millefolium</i>	77	95	>16	>16	
<i>Aegopodium podagraria</i>	39	95	>17	>17	
<i>Aethusa cynapium</i>	11	73	2	2	2
<i>Agrostis canina</i>	81	86	>19	>19	
<i>Agrostis capillaris</i>	225	93	>21	>21	
<i>Agrostis stolonifera</i>	131	82	10	>15	
<i>Agrostis vinealis</i>	22	95	16	>16	
<i>Aira praecox</i>	10	20	1	1	2
<i>Ajuga reptans</i>	13	69	4	10	
<i>Alopecurus geniculatus</i>	21	38	1	1	
<i>Alopecurus myosuroides</i>	17	24	1	3	3
<i>Alopecurus pratensis</i>	10	80	6	5	
<i>Anagallis minima</i>	10	40	2	6	9
<i>Anagallis tenella</i>	10	70	6	6	
<i>Angelica archangelica</i>	15	40	1	4	5
<i>Angelica sylvestris</i>	111	72	4	>15	
<i>Anthoxanthum odoratum</i>	221	91	>21	>21	
<i>Anthriscus sylvestris</i>	39	62	2	>15	
<i>Apera spica-venti</i>	10	50	1	1	
<i>Aphanes inexpectata</i>	10	20	1	3	5
<i>Arabidopsis thaliana</i>	12	42	1	1	3
<i>Arenaria serpyllifolia</i>	24	17	1	1	4
<i>Arrhenatherum elatius</i>	90	97	>16	>16	
<i>Asparagus officinalis</i>	14	36	1	2	
<i>Bellis perennis</i>	32	63	1	>15	
<i>Berula erecta</i>	17	71	2	>15	
<i>Blackstonia perfoliata</i>	14	50	2	2	6
<i>Blysmus compressus</i>	18	83	>20	>20	
<i>Briza media</i>	38	92	>16	>16	
<i>Bromus hordeaceus</i> subsp. <i>hordeaceus</i>	81	43	1	5	12
<i>Calamagrostis epigejos</i>	54	78	6	>15	
<i>Calluna vulgaris</i>	23	96	>18	>18	
<i>Caltha palustris</i>	24	63	2	14	
<i>Calystegia sepium</i>	95	80	11	>15	
<i>Campanula rapunculus</i>	32	66	1	>15	
<i>Campanula rotundifolia</i>	18	89	>14	>14	
<i>Capsella bursa-pastoris</i>	54	67	2	2	
<i>Cardamine amara</i>	18	44	2	3	
<i>Cardamine hirsuta</i>	56	43	1	3	9
<i>Cardamine pratensis</i>	156	78	6	>15	
<i>Carduus crispus</i>	10	10	1	1	3
<i>Carex arenaria</i>	80	98	>18	>18	
<i>Carex disticha</i>	41	76	3	>15	
<i>Carex flacca</i>	47	83	8	>15	
<i>Carex hirta</i>	82	83	>19	>19	
<i>Carex nigra</i>	70	74	4	>15	
<i>Carex oederi</i> subsp. <i>oederi</i>	75	88	>18	>18	
<i>Carex ovalis</i>	81	74	5	>15	
<i>Carex panicea</i>	50	76	6	>15	
<i>Carex remota</i>	15	27	1	5	7
<i>Carex trinervis</i>	43	79	6	6	
<i>Carex x timmiana</i>	18	78	>6	>15	

Species name	N _{plots}	% Censored	T ₇₅	T ₅₀	T ₂₅
<i>Centaurea jacea</i>	57	91	>17	>17	
<i>Centaurium erythraea</i>	40	43	2	6	
<i>Centaurium littorale</i>	30	70	4	>15	
<i>Centaurium pulchellum</i>	20	55	1	3	4
<i>Cerastium arvense</i>	25	80	>16	>16	
<i>Cerastium fontanum</i>	204	64	2	15	
<i>Cerastium glomeratum</i>	69	30	1	2	3
<i>Cerastium semidecandrum</i>	20	25	2	3	6
<i>Chamerion angustifolium</i>	95	69	5	>15	
<i>Chenopodium album</i>	38	79	>3	>15	
<i>Chenopodium polyspermum</i>	11	82	>1		
<i>Cirsium arvense</i>	72	74	5	>15	
<i>Cirsium palustre</i>	128	64	2	>15	
<i>Cirsium vulgare</i>	60	38	1	2	5
<i>Conyza canadensis</i>	75	23	1	3	5
<i>Corynephorus canescens</i>	49	90	>18	>18	
<i>Crataegus monogyna</i>	110	62	2	7	
<i>Crepis biennis</i>	14	86	>8	>8	
<i>Crepis capillaris</i>	57	51	1	4	
<i>Cynosurus cristatus</i>	40	73	4	12	
<i>Dactylis glomerata</i>	88	73	6	>15	
<i>Dactylorhiza incarnata</i>	30	73	8	>15	
<i>Dactylorhiza maculata</i>	10	90	>9	>15	
<i>Danthonia decumbens</i>	13	69	1	>5	
<i>Daucus carota</i>	52	58	3	12	
<i>Deschampsia flexuosa</i>	47	91	>20	>20	
<i>Digitalis purpurea</i>	20	60	3	5	
<i>Echinodorus ranunculoides</i>	12	58	1	>5	
<i>Eleocharis palustris</i>	81	75	3	>15	
<i>Eleocharis quinqueflora</i>	25	48	2	3	10
<i>Elytrigia repens</i>	122	93	>16	>16	
<i>Epilobium hirsutum</i>	17	65	2	>15	
<i>Epilobium montanum</i>	11	9	1	2	2
<i>Epilobium palustre</i>	44	68	3	>15	
<i>Epilobium parviflorum</i>	52	52	1	4	
<i>Epilobium tetragonum</i>	113	35	2	4	6
<i>Epipactis palustris</i>	41	78	8	>15	
<i>Equisetum arvense</i>	187	75	7	>15	
<i>Equisetum fluviatile</i>	11	36	1	2	3
<i>Equisetum palustre</i>	91	70	3	>15	
<i>Equisetum variegatum</i>	33	76	11	>15	
<i>Erigeron acer</i>	17	59	1	>15	
<i>Erodium cicutarium</i>	13	23	1	3	5
<i>Erophila verna</i>	24	25	1	3	9
<i>Eupatorium cannabinum</i>	84	79	6	>15	
<i>Euphorbia exigua</i>	12	33	1	2	2
<i>Euphorbia helioscopia</i>	28	64	2	2	3
<i>Euphrasia stricta</i>	75	60	2	9	
<i>Fallopia convolvulus</i>	20	85	2	>15	
<i>Festuca arundinacea</i>	38	76	>17	>17	
<i>Festuca ovina</i> agg.	46	85	>17	>17	
<i>Festuca pratensis</i>	16	63	2	7	
<i>Festuca rubra</i> agg.	214	92	>21	>21	
<i>Fragaria vesca</i>	28	82	13	13	
<i>Fragaria x ananassa</i>	24	46	1	5	
<i>Galeopsis tetrahit</i>	34	44	1	3	
<i>Galium aparine</i>	57	53	1	6	
<i>Galium mollugo</i>	24	92	>15	>15	
<i>Galium palustre</i>	88	76	6	>15	

Species name	N _{plots}	% Censored	T ₇₅	T ₅₀	T ₂₅
Galium uliginosum	68	74	4	>15	
Galium verum	26	81	>16	>16	
Gentianella amarella	44	61	2	8	
Geranium dissectum	43	16	1	2	5
Geranium molle	23	96	>7	>15	
Glaux maritima	22	73	3	>15	
Glechoma hederacea	84	94	>19	>19	
Glyceria fluitans	10	80	3	>5	
Gnaphalium luteo-album	14	57	1	4	
Gnaphalium uliginosum	35	63	2	2	4
Helictotrichon pubescens	48	83	>15	>15	
Heracleum sphondylium	55	82	>21	>21	
Hieracium pilosella	47	98	>14	>14	
Hippophae rhamnoides	63	63	2	8	
Holcus lanatus	280	73	6	>15	
Holcus mollis	121	98	>21	>21	
Hydrocotyle vulgaris	100	88	>25	>25	
Hypericum dubium	21	52	6	7	
Hypericum humifusum	17	24	1	2	3
Hypericum perforatum	39	51	3	7	13
Hypericum tetrapterum	19	74	3	>15	
Hypochaeris radicata	137	72	7	>15	
Impatiens noli-tangere	12	25	1	1	3
Jasione montana	40	58	1	8	10
Juncus acutiflorus	60	98	>21	>21	
Juncus articulatus	71	77	8	>15	
Juncus bufonius	53	57	1	3	
Juncus bulbosus	10	40	2	3	6
Juncus conglomeratus	63	63	2	>15	
Juncus effusus	124	76	8	>15	
Juncus gerardii	38	71	5	>15	
Juncus subnodulosus	13	54	1	8	8
Knautia arvensis	52	90	>16	>16	
Koeleria macrantha	31	90	>14	>14	
Lamium hybridum + L. purpureum	41	56	2	2	6
Lapsana communis	15	40	1	4	
Lathyrus pratensis	23	83	4	>15	
Lathyrus tuberosus	11	64	2	>5	
Leontodon autumnalis	23	39	1	3	7
Leontodon hispidus	47	96	>17	>17	
Leontodon saxatilis	18	56	1	3	
Leucanthemum vulgare	98	97	>20	>20	
Ligustrum vulgare	20	45	1	1	
Linum catharticum	59	71	3	>15	
Liparis loeselii	30	63	2	4	
Littorella uniflora	14	64	3	>15	
Lolium perenne	75	56	2	7	16
Lotus corniculatus	41	80	7	>15	
Lotus pedunculatus	124	74	5	>15	
Luzula campestris	188	90	>20	>20	
Luzula multiflora	49	84	7	>15	
Lycopus europaeus	57	77	7	>15	
Lysimachia vulgaris	46	85	>16	>16	
Lythrum salicaria	45	62	2	10	
Matricaria recutita	29	48	1	3	4
Medicago lupulina	33	94	>16	>16	
Mentha aquatica	102	92	>25	>25	
Moehringia trinervia	23	30	1	2	7
Molinia caerulea	39	87	>18	>18	

Species name	N _{plots}	% Censored	T ₇₅	T ₅₀	T ₂₅
Myosotis arvensis	85	40	2	4	9
Myosotis discolor	91	20	1	2	3
Myosotis laxa (subsp. cespitosa)	45	69	2	9	9
Myosotis ramosissima	26	23	1	3	9
Myosotis scorpioides	17	35	1	4	11
Oenanthelachenalii	23	57	1	6	10
Oenothera biennis	56	52	2	6	
Ononis repens	51	89	>17	>17	
Ornithopus perpusillus	20	40	1	2	
Oxalis fontana	68	53	2	3	
Papaver dubium	24	21	1	1	3
Papaver rhoeas	39	44	1	2	5
Parnassia palustris	54	81	8	>15	
Pastinaca sativa	18	72	5	>15	
Persicaria hydropiper	15	73	5	15	15
Persicaria maculosa	20	80	3	>15	
Peucedanum palustre	13	92	>10	>10	
Phalaris arundinacea	10	60	7	10	
Phleum pratense	33	61	6	16	
Phragmites australis	117	85	16	>16	
Pimpinella saxifraga	34	94	>11	>11	
Plantago lanceolata	71	76	6	>15	
Plantago major subsp. intermedia	16	75	5	>15	
Plantago major subsp. major	52	67	3	8	
Poa annua	74	62	2	4	
Poa palustris	10	50	2	2	
Poa pratensis	278	80	>25	>25	
Poa trivialis	212	70	4	>15	
Polygala vulgaris	15	73	1	>15	
Polygonum aviculare	25	64	2	2	
Potentilla anserina	46	72	5	>15	
Potentilla erecta	37	95	>19	>19	
Potentilla palustris	18	78	3	>15	
Potentilla reptans	46	78	6	>15	
Primula veris	12	83	>15	>15	
Prunella vulgaris	122	77	6	>15	
Pulicaria dysenterica	27	67	1	>15	
Pyrola rotundifolia	13	69	3	>5	
Ranunculus acris	178	88	>21	>21	
Ranunculus bulbosus	31	81	7	>15	
Ranunculus ficaria	37	73	3	>15	
Ranunculus flammula	63	73	3	>15	
Ranunculus repens	268	86	>25	>25	
Rhamnus cathartica	44	52	1	5	
Rhamnus frangula	14	64	2	6	
Rhinanthus angustifolius	21	76	2	>15	
Rhinanthus minor	38	97	12	>15	
Rosa pimpinellifolia	20	90	>8	>15	
Rubus caesius	102	65	2	14	
Rubus fruticosus	31	42	2	4	12
Rubus idaeus	19	47	2	6	
Rumex acetosa	234	92	>21	>21	
Rumex acetosella	92	71	5	>15	
Rumex crispus	43	49	2	6	
Rumex obtusifolius	79	96	>15	>15	
Sagina nodosa	49	78	7	>15	
Sagina procumbens	48	40	1	2	
Samolus valerandi	24	79	6	>15	
Scrophularia nodosa	31	68	6	>15	

Species name	N _{plots}	% Censored	T ₇₅	T ₅₀	T ₂₅
<i>Scutellaria galericulata</i>	14	64	1	>5	
<i>Sedum acre</i>	13	85	>18	>18	
<i>Senecio erucifolius</i>	24	38	2	9	13
<i>Senecio jacobaea</i>	119	64	3	15	
<i>Senecio viscosus</i>	17	6	1	1	2
<i>Senecio vulgaris</i>	12	50	1	2	
<i>Silene dioica</i>	12	50	4	10	11
<i>Sinapis arvensis</i>	12	67	1	2	
<i>Solanum dulcamara</i>	29	34	1	3	4
<i>Sonchus arvensis</i>	27	56	1	3	
<i>Sonchus asper</i>	49	59	1	3	
<i>Sonchus oleraceus</i>	24	63	1	2	
<i>Spergula morisonii</i>	11	45	2	3	
<i>Stachys sylvatica</i>	14	50	2	6	9
<i>Stellaria graminea</i>	71	77	3	>15	
<i>Stellaria media</i>	72	61	2	2	
<i>Symphytum officinale</i>	78	87	>16	>16	
<i>Taraxacum officinale</i>	184	73	6	17	
<i>Teesdalia nudicaulis</i>	41	54	1	7	
<i>Thymus pulegioides</i>	16	94	>16	>16	
<i>Tragopogon pratensis</i>	19	74	2	>15	
<i>Trifolium dubium</i>	85	55	1	6	
<i>Trifolium fragiferum</i>	37	54	3	7	
<i>Trifolium pretense</i>	68	63	3	>15	
<i>Trifolium repens</i>	189	76	4	>15	
<i>Tripleurospermum maritimum</i>	22	32	1	2	5
<i>Trisetum flavescens</i>	54	78	5	>15	
<i>Tussilago farfara</i>	25	64	5	10	
<i>Urtica dioica</i>	85	93	>30	>30	
<i>Valeriana officinalis</i>	21	52	1	14	14
<i>Verbascum densiflorum</i>	10	30	3	3	5
<i>Veronica agrestis</i>	16	50	1	2	2
<i>Veronica arvensis</i>	91	41	2	3	8
<i>Veronica chamaedrys</i>	90	89	>16	>16	
<i>Veronica officinalis</i>	12	50	6	7	13
<i>Veronica persica</i>	10	50	2	2	3
<i>Veronica serpyllifolia</i>	37	41	1	4	7
<i>Vicia cracca</i>	27	67	2	>15	
<i>Vicia hirsuta</i>	98	41	1	3	8
<i>Viola arvensis</i>	24	29	1	1	3
<i>Viola curtisii</i>	14	36	2	7	9



Dispersal potential in plant communities depends on environmental conditions

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Journal of Ecology 92: 767–777.

The diet of Bohemian Waxwing (*Bombycilla garrulus*) consists primarily of berries and this bird species can be an effective vector for long-distance seed dispersal. For some shrub species with bitter tasting fruits, like Guelder Rose (*Viburnum opulus*), it can be one of the main dispersal vectors (photo L. Hoogenstein).

Abstract

Local plant communities can only function within a metacommunity context if they are connected by appropriate dispersal vectors, accommodating the transport of propagules between sites. The capacity for long-distance dispersal may be a key factor in the survival of local populations, especially in fragmented landscapes, and hence may have a large impact on local species composition. Dispersal vectors with a large efficiency for long-distance dispersal included in this study are: water, wind, large mammals and birds.

We tested the hypothesis that variation in dispersal traits across plant communities is related to the position of the communities along major environmental gradients. This hypothesis was tested for (1) separate long-distance dispersal vectors and (2) multiple dispersal vectors (the number of potential long-distance dispersal vectors per species).

To quantify linkages between dispersal traits and environmental gradients, we coupled a database containing dispersal attributes with another database, containing 40,000 local vegetation descriptions aggregated into 123 plant communities. For each dispersal vector, the proportions of species that have access to this vector per community (weighted trait scores) were projected along three major environmental gradients: soil moisture, nutrient availability and light availability.

The potential importance of individual dispersal vectors showed clear differences along the three environmental gradients, with the greatest differences along the light availability gradient. The differences in dispersal traits probably reflect environmental constraints on the availability or efficiency of individual dispersal vectors.

The ability to be dispersed by multiple dispersal vectors is a common phenomenon in most plant communities (an average of 2.15 vectors per species). The mean number of potential long-distance dispersal vectors per species increases with light availability. This probably implies that plant communities differ in their response to both habitat fragmentation and habitat restoration.

Despite differences in trait spectra among communities, all dispersal syndromes are represented in nearly all communities. An important consequence of this complementarity in dispersal traits is that species within the same community may experience different connectivity.

The results emphasize the need for dispersal models based upon multiple dispersal vectors that explicitly include parameters for habitat characteristics.

Introduction

Given a certain set of environmental conditions, the community composition at a site is influenced by both the rates of local extinction and the rates of colonization from the species pool (e.g. Freckleton & Watkinson 2002). It follows from basic metapopulation theory (Levins 1969; Hanski 1998) that species within a meta-community (sets of communities connected by dispersal of component species; Mouquet & Loreau 2002) occupy only a fraction of the suitable habitat patches because species continually become locally extinct and these sites may not be re-occupied if colonization capacity is limited, at least at larger spatial scales. Within local communities, there is thus a continuous turnover of species, as has been demonstrated by detailed field observations in grasslands by Van der Maarel & Sykes (1993). Seed sowing experiments have underpinned the notion that dispersal limitation is almost universal in plant communities (Turnbull et al. 2000; Foster & Tilman 2003; Xiong et al. 2003). Interspecific differences in dispersal traits are therefore expected to affect local species composition.

Short-distance dispersal (i.e. within local populations) will generally be sufficient for the local survival of populations in habitats with a high level of spatial and temporal continuity. But in spatially heterogeneous landscapes (such as in many industrialized parts of the world) the survival probability of local populations increases for species that have higher rates of long-distance dispersal. Studies by Ellstrand & Elam (1993), Ouborg (1993) and Harrison et al. (2000) indicate that species in patches that are more isolated have a higher probability of becoming locally extinct, and such patches have a lower probability of becoming colonized or recolonized. The emphasis in our study was therefore on long-distance dispersal, which we define as dispersal between sites separated by more than 100 m, following Cain et al. (2000).

At the species level, there are large interspecific differences in seed attributes which determine the potential of the various dispersal modes to serve as long-distance dispersal vectors (e.g. Cain et al. 2000; Pakeman et al. 2002; Tackenberg et al. 2003). Moreover, species differ not only in the efficiency of dispersal by different dispersal vectors, but also in the number of dispersal vectors by which they are potentially dispersed between sites (specialists vs. generalists for long-distance dispersal or with no adaptations for long-distance dispersal at all), but reliable quantifications of this variation are lacking.

Interspecific differences in dispersal traits can be integrated at the community level by quantifying the proportions of potential dispersal vectors. There have been few studies on differences in dispersal traits between habitats (Gentry 1983; Willson et al. 1989; Willson et al. 1990; Hughes et al. 1994) and these studies show methodological limitations as both dispersal traits and habitat characteristics are poorly defined. The recent compilation of large databases on community composition and on dispersal attributes for species offers new opportunities to quantify the relationship between environmental conditions and dispersal traits.

Linking species composition and data on dispersal attributes may improve our understanding of the interactions between local (<100m) and regional (>100m) processes.

The assembly of local communities from a given species pool is generally studied by means of two complementary approaches, relating to different scales. At the local scale, the so-called ‘niche assembly view’ focuses on interactions between individuals of different species and interspecific niche differences. According to this view, the species composition of a community is a deterministic consequence of physiological processes and biological interactions (e.g. MacArthur & Connell 1966; Tilman 1985; Keddy 1992). On the other hand, the so-called ‘dispersal assembly view’ focuses on larger scales, both in space and time, and assigns a more prominent role to stochastic events such as catastrophic changes in environmental conditions, local extinction and long-distance dispersal (e.g. MacArthur & Wilson 1967; Zobel 1997; Turnbull et al. 2000).

If environmental conditions constrain the availability or efficiency of individual dispersal vectors (cf. Grubb 1987), differences may be expected between communities with regard to dispersal attributes. If the relative importance of dispersal vectors is indeed influenced by environmental conditions, this implies that there is an uneven dispersal potential across landscapes dependent on the distribution of habitats. This will in turn affect the community assembly processes that determine local species composition and biodiversity. Linkages between dispersal traits and environmental gradients imply that communities will differ in their response to habitat fragmentation and habitat restoration.

We tested the hypothesis that variation in dispersal traits across plant communities is related to the position of communities along major environmental gradients. This hypothesis was tested for (1) the distribution of individual dispersal vectors in plant communities and (2) the degree to which species within communities are served by multiple dispersal vectors.

Materials and methods

Our approach is based on combining large databases containing species-level dispersal traits and environmental optima with those for community-level species co-occurrence. An overview of the database linkages is given in Fig. 5.1.

Dispersal attribute database

The efficiency of various dispersal vectors for a given species can be classified based either on differences in actually realized dispersal distance or on differences in attributes that (potentially) give access to dispersal modes with a high efficiency for long-distance dispersal (Muller-Landau et al. 2003). Long-distance dispersal (>100 m, cf. Cain et al. 2000) depends on the tail of the ‘dispersal kernel’ and is extremely difficult to quantify (Cain et al. 2000; Bullock & Clarke 2000; Nathan & Muller-

Landau 2000). The probability of ending up in the tail of the dispersal kernel is not only dependent on species traits, but also on landscape characteristics, such as vegetation structure, presence of barriers and availability of dispersal vectors. Even perfect information on the dispersal distance of all seeds in a population would only provide a case-specific documentation of differences in realized dispersal distance (Tackenberg et al. 2003; Nathan et al. 2003). Realistic, mechanistic models, are only available for dispersal by wind (e.g. Nathan et al. 2002; Tackenberg et al. 2003; Soons et al. 2004), but are lacking for other dispersal vectors. It is therefore not realistic to quantify the probability of seeds dispersing over distances of >100m for many species under various conditions for all dispersal vectors.

On the other hand, differences in attributes that determine the degree of access to various dispersal modes can be quantified more easily (Weiher et al. 1999; Pakeman et al. 2002; Boedeltje et al. 2003; Tackenberg et al. 2003; Cornelissen et al. 2003, Knevel et al. 2003, 2005). Therefore we have adopted a trait-based approach, and have compiled a database for the Dutch flora, with plant and propagule traits that are relevant to dispersal. Raw data were extracted from the LEDA database (Knevel et al. 2003, 2005, Kleyer et al. in prep.). We consider the following dispersal vectors to have a high efficiency for long-distance dispersal (for further details see Chapter 2): water (*hydrochory*), wind (*anemochory*), attachment to the fur of large mammals (*epizoochory by mammals*), survival in the digestive tract of large mammals (*endozoochory by mammals*) and frugivorous birds (*endozoochory by birds*). The degree to which species have access to these dispersal vectors is inferred from morphological and physical traits that have been shown to be related to the efficiency of dispersal by the various vectors (Weiher et al. 1999; Pakeman et al. 2002; Boedeltje et al. 2003; Tackenberg et al. 2003; Cornelissen et al. 2003; see Chapter 2 for a detailed explanation for each dispersal vector). This provides us with a relative classification of the potential of species for dispersal by various vectors that is independent of landscape characteristics, climatological conditions and the number of seeds produced. In order to include as many species as possible and to facilitate comparisons between different dispersal vectors, we aggregated the available data into a binary classification, assigning each species to one of two classes for each dispersal agent: '1' if the species has attributes that give access to a given vector and '0' if the species has no such attributes (see Chapter 2 for criteria). This resulted in a species-by-trait matrix (*matrix 1* in Fig. 5.1). Although the binary classification of the continuum is relatively imprecise for individual species, it allows generalizations to be made at the community level across habitats.

It is important to note that many species have a high dispersal potential (i.e. a '1' in the database) for more than one long-distance dispersal vector. These species can be regarded as generalists in terms of long-distance dispersal. On the other hand, several species have low potential for all five long-distance dispersal vectors (although many of them have special adaptations for short-distance dispersal, such as mechanisms to release seeds ballistically or nutrient-rich appendages to attract

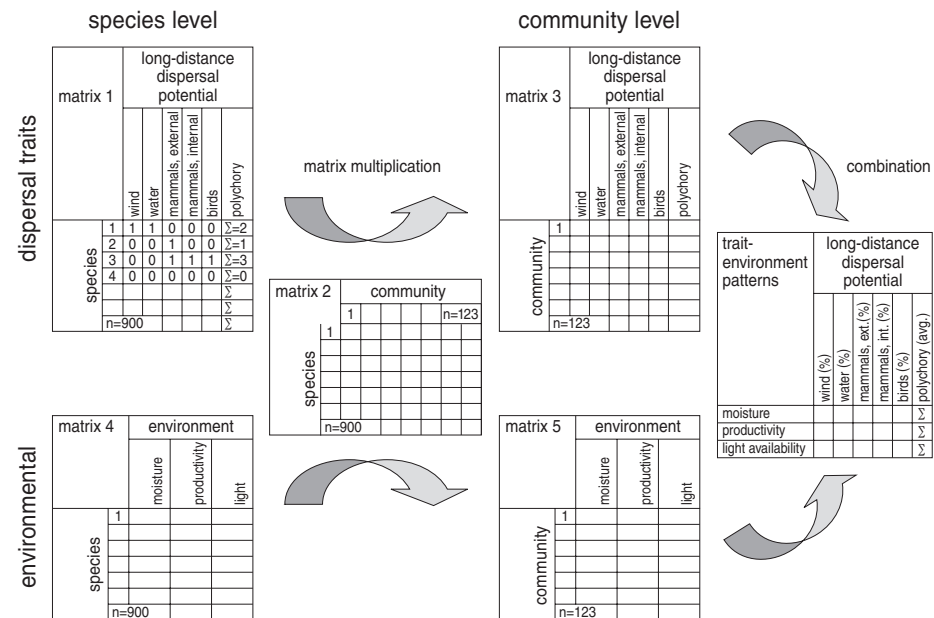


Figure 5.1: Overview of the database linkages needed for the establishment of the trait-by-environment pattern. Matrices 1 and 4 contain data at the species level for dispersal potential (matrix 1) and the optimum occurrence along environmental gradients as expressed by Ellenberg indicator values (matrix 4). Both matrices were multiplied by the species-by-community matrix (matrix 2) to calculate weighted means at the community level (matrix 3 and 5). The data from matrices 1 and 4 have been weighted by the % presence of the species within the communities (in the cells of matrix 2, based on 40,000 local plot descriptions). Combining matrix 3 (percentage of species within communities with a high potential for dispersal by each dispersal vector) and matrix 5 (position of communities along the three major environmental gradients) results in a set of relationships between environmental gradients (x-axis) and dispersal traits (y-axis). This combination of large ecological databases on different organisational levels to reveal new information can be regarded as an example of ‘ecoinformatics’.

ants). To summarize this information, we included a field with the number of long-distance dispersal vectors per species (a summation of the scores for the five dispersal vectors; see matrix 1 in Fig. 5.1). For dispersal in general, potential dispersal by multiple agents has been termed ‘polychory’ (e.g. Ridley 1930; Van der Pijl 1982), but since we restricted our analysis to dispersal vectors with a high efficiency for long-distance dispersal, we called this aggregated trait ‘long-distance polychory’. Although *long-distance polychory* is probably closely related to total long-distance dispersal potential, it is not exactly the same and merely reflects the number of possible types of vectors for long-distance dispersal.

A total of 900 vascular plant species (ca. 75% of the total terrestrial flora of the Netherlands) were included in the analysis. Trees, spore-plants and orchids were excluded.

Vegetation Database

We quantified the proportions of species that have access to specific dispersal vectors at the community level using the Dutch Vegetation Database (Hennekens & Schaminée 2001, see Box 2 in Chapter 1), which comprises over 400,000 descriptions of species composition at specific plots ($<100\text{m}^2$) throughout the Netherlands. The Dutch vegetation classification (Schaminée et al 1995-1999), uses cluster analysis to analyse a subset of 40,000 plots, and assign them to 228 plant communities. We made a further selection to exclude plant communities occurring in saline and aquatic environments, to give a simpler database representing terrestrial plant diversity in the Netherlands. This compressed the information into a species-by-community matrix (*matrix 2* in Fig. 5.1) with 123 plant communities and 900 plant species, in which each cell contained the percentages of plots for a given community in which the species was present (% presence).

Dispersal attributes within communities

Combining the species-by-trait database (matrix 1) with the species-by-community matrix (matrix 2) allowed us to quantify patterns of dispersal traits at the community level (community-by-trait matrix; *matrix 3*). The proportions of species that have access to specific dispersal vectors (trait scores) were weighted according to the percentage of plots in which the species were present (abundance in the 'habitat species pool').

Position of communities along environmental gradients

We characterized the environmental conditions of communities using Ellenberg indicator values (species-by-environment matrix; *matrix 4*). These indicator values give the ecological optima of species for a range of abiotic parameters and were obtained from Ellenberg et al. (1992). Evidence for the accuracy of the indicator values has been provided by several studies reporting close correlations between average indicator values and corresponding measurements of environmental variables (e.g. Thompson et al. 1993; Schaffers & Sýkora 2000; Diekmann 2003). Multiplying the species-by-environment matrix (matrix 4) by the species-by-community matrix (matrix 2) resulted in a community-by-environment matrix (*matrix 5*) in which the position of each community is quantified relative to the three major environmental gradients. The Ellenberg indicator values were weighted with the percentage of plots in which the species were present.

We used two complementary ordination methods (DCA and CCA) to reveal relationships between the species-by-community matrix (matrix 2) and the community-by-environment matrix (matrix 5). Variation in species composition of terrestrial plant communities in the Netherlands was mainly related to three major environmental gradients (Ozinga et al. 2005b), reflecting differences in the availability of water and oxygen, of nutrients and of light and open space. We restricted our analysis to these three environmental variables between which community-level correlations were low ($r < 0.25$; Ozinga et al. 2005b).

Trait-environment linkages

Finally, relationships between the distribution of the five dispersal traits over the three major environmental gradients were quantified at both the species level and the community level. At the species level this was achieved by the combination of matrices 1 and 4.

At the community level the trait-environment patterns were quantified by the linkages between the community-dispersal trait database (matrix 3) and the community-environment database (matrix 5; Fig. 5.1). We also calculated the mean number of long-distance dispersal vectors per species within each community ('long-distance polychory index'). In comparison to the species level analysis, the community level analyses are less sensitive to misclassifications in the original Ellenberg indicator values (e.g. Diekmann 2003) and account for inter-specific differences in regional abundance (species-trait combinations of very rare species are given less weight than those of common species).

Statistical analyses were conducted on the trait-environment data using SPSS 10.0 (© SPSS Inc. 1989-1999). Relationships between the trait scores and the three main environmental gradients (availability of water, nutrients and light) were tested for significance for each dispersal vector separately. For the analyses at the species level we used stepwise logistic regression and for the analyses at the community level we used stepwise multiple regression.

Results

An overview of the regression models for each dispersal vector is given in Table 5.1 for the species level (not weighted by regional abundance) and in Table 5.2 for the community level. The directions of the relationships between dispersal traits and environmental conditions at the species level were consistent with the results at the community level. At the community level, however, the patterns were much more pronounced (Table 5.1 vs. Table 5.2), as indicated by higher beta-values and higher proportions of explained variance (R^2 -values). At the community level the R^2 -values were, in general, more than 10 times as high as those at the species level. Different dispersal vectors were only weakly correlated among species ($r < 0.30$ for all combinations; data not shown).

The strongest trait-environment linkages ($R^2_{\text{change}} > 0.25$) at the community level are illustrated in Fig. 5.2. In the panels of this figure, each point represents a plant community. The x-axes give the position of the communities relative to the environmental gradient as indicated by Ellenberg indicator values (mean for communities weighted by the percentage of plots in which each of the species was present), while the y-axes give the trait scores for each community (also weighted by the % presence).

The differences in the potential importance of individual dispersal vectors were greatest along the light availability gradient, and all of the dispersal vectors,

Table 5.1: Significant trait-environment relationships at the species level. Binary logistic regression models were performed with the dispersal traits as the dependent variable and the Ellenberg indicator values for moisture, nutrient availability and light availability as independent variables. Models are based on the total species pool (N=900). The percentage of variance explained is approximated with Nagelkerke's R^2 (comparable to the R^2 values in the linear regressions in table 5.2).

Dispersal vector	independent variable	Beta (standardized)	Nagelkerke R^2	Sig. (G-test)
Water	moisture	0.49	0.300	<0.001
Wind	nutrient availability	-0.15	0.036	<0.001
Mammals, externally	light availability	0.17	0.013	0.002
Mammals, internally	light availability	0.15	0.014	0.001
Birds, internally	light availability	-0.36	0.050	<0.001

Table 5.2: Significant trait-environment relationships at the community level. Linear regression models were performed with the proportion of species that have access to a given dispersal vector as the dependent variable and the positions of communities along environmental gradients as independent variables. All models are based on 123 terrestrial plant communities. Environmental variables are given in order of entrance into the model. The R^2_{adj} values refer to the total model, while Sig. R^2_{change} refers to the significance of the change in R^2 after entering the variable in the model. Explanatory variables were only included if the proportion of explained variance increased significantly (Sig. R^2_{change} : $p < 0.05$).

	environmental variable entered in model	Beta (standardized)	R^2_{adj}	Sig. R^2_{change}
Water	moisture	0.92	0.84	<0.001
Wind	nutrient availability	-0.66	0.38	<0.001
	light availability	0.36	0.50	<0.001
	moisture	0.14	0.52	0.040
Mammals, externally	light availability	0.64	0.41	<0.001
	nutrient availability	-0.20	0.44	0.005
Mammals, internally	light availability	0.73	0.53	<0.001
	nutrient availability	0.18	0.56	0.004
Birds, internally	light availability	-0.77	0.57	<0.001
	nutrient availability	-0.19	0.61	0.001
Long-distance polychory	light availability	0.6	0.34	<0.001
	moisture	0.55	0.59	0.000
No adaptations	light availability	-0.50	0.23	<0.001
	moisture	-0.47	0.33	<0.001
	nutrient availability	0.43	0.48	0.008

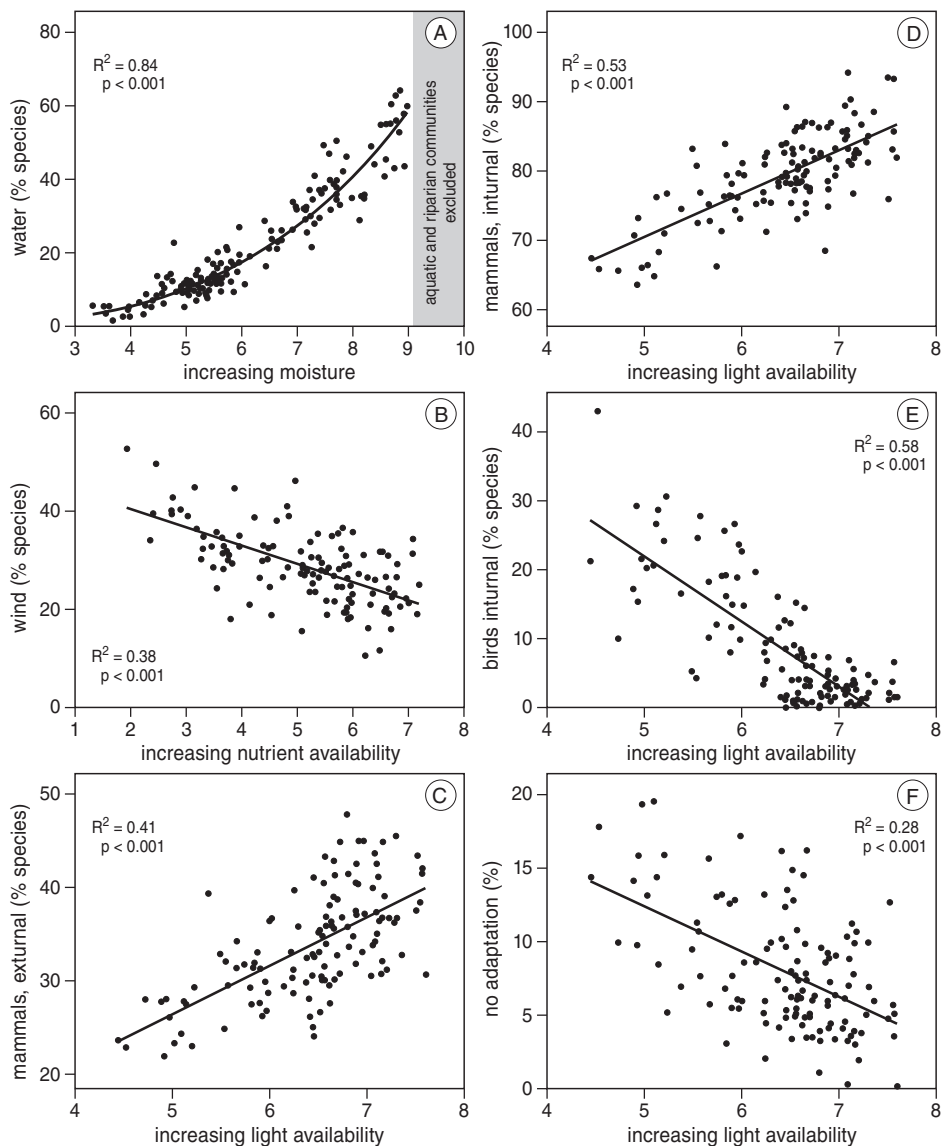


Figure 5.2: Overview of relationships between dispersal traits and environmental gradients. All combinations of long-distance dispersal vectors ($N=5$) and the major environmental gradients ($N=3$) with a $R^2_{\text{change}} > 0.25$ are given (see Table 5.2). The graphs show the proportion of species with a high potential for dispersal by, respectively: (A) water, (B) wind, (C) fur of large mammals, (D) dung of large mammals and (E) birds. Panel f shows the proportion of species without any adaptations for long distance dispersal vectors. In these panels each point represents a plant community ($N=123$). The x-axis shows the position of the communities relative to the environmental gradient as indicated by Ellenberg indicator values (mean for communities weighted by the frequency of occurrence of the species). The y-axis shows the percentage of species within each community with a high potential for dispersal by the dispersal vector under consideration.

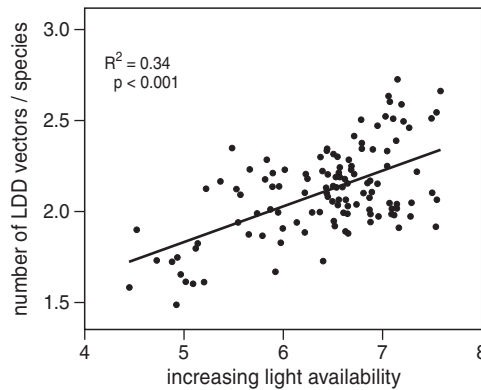


Figure 5.3: Mean number of potential long-distance dispersal (LDD) vectors per species within each community (long-distance polychory index) relative to the position along the light availability gradient.

except water, showed significant positive relationships with light availability (Table 5.2). Both epizoochorous and endozoochorous dispersal by mammals became more important with increasing light availability (Fig. 5.2C and D). The proportion of species with a high potential for dispersal by frugivorous birds (Fig. 5.2E) and the proportion of species with no adaptations for long-distance dispersal at all (Fig. 5.2F) showed the opposite pattern, decreasing significantly with increasing light availability. The variation in the potential for dispersal by water can be largely explained by soil moisture ($R^2 = 0.84$; Fig. 5.2A). Changes in the potential of wind as a dispersal vector were most closely related to nutrient availability (Fig. 5.2B) and, to a smaller extent, to light availability. Although some other long-distance dispersal vectors were significantly related to nutrient availability, the increases in the explained variance due to this environmental trait were small ($R^2_{\text{change}} < 0.05$). Despite the differences in relative importance of individual dispersal vectors, all dispersal syndromes are represented in many communities (although sometimes with low proportions; Fig. 5.2), such that, in 70% of communities, all dispersal vectors are represented by at least 5% of the species. Many species in the Dutch flora have the potential to be dispersed over long distances by more than one dispersal vector (long-distance polychory). The average number of dispersal vectors per species for all 900 species was 1.57. Weighted by the frequency of occurrence in each community, the average becomes 2.15 vectors per species. The average number of long-distance dispersal vectors per species within the communities (long-distance polychory index) was found to decrease with decreasing availability of light (Fig. 5.3), thus showing the opposite trend to the proportion of species that have no access to any of the long-distance dispersal vectors (2F). The average number of long-distance dispersal vectors per species within a community was not related to nutrient availability (Table 5.2).

Discussion

Environmental constraints on the availability and efficiency of dispersal vectors

The results show clear differences in the potential importance of the various dispersal vectors along the major environmental gradients, both at the species level and at the community level. The non-random distribution of dispersal traits along environmental gradients supports the hypothesis that the potential importance of the various dispersal vectors depends on the environmental context. The patterns were much stronger at the community level (higher Beta and R^2 -values; Table 5.1 vs. 5.2). This can be explained by a non-random selection of species assemblages from the regional species pool with regard to dispersal traits. In a complementary study (Ozinga et al. 2005; chapter 3) we have shown that species with high dispersal ability are indeed over-represented in local plots in comparison to a random selection of species from the habitat species pool. In the present paper our main interest is not the difference between the species level and the community level results, but merely the differences in dispersal traits across environmental gradients.

WATER

The close correlation ($R^2 = 0.84$) between the position of a plant community along the moisture gradient and the percentage of species with a high potential for dispersal by water indicates that dispersal by water can be important in determining species composition within wet communities. This can be explained by the high efficiency of water as a dispersal vector in frequently inundated sites, in combination with the relatively high gap dynamics in landscapes where parts of the vegetation are regularly destroyed by inundation and/or sedimentation, increasing the availability of safe sites for establishment. These results are in agreement with the findings of Boedeltje et al. (2003).

An unexpected finding was that even in communities with intermediate soil moisture levels (mean Ellenberg values 6-8) the percentage of species that can be dispersed by water is still as high as 20-40% (both at the species level and at the community level). This illustrates that, although inundations in these communities may be occasional, the impact on species composition is potentially large. Dry storage of seeds (e.g. remaining attached to the mother plant during winter) increases the floating ability of the seeds of several species (Praeger 1913; Bill et al. 1999), probably due to shrinkage of the fruit content relative to the fruit surface, seed coat hardening and increased water-repellency (Baskin & Baskin 1998). Increased impermeability of the seed coat during maturation induces seed dormancy in these species, and may, in dry environments, lead to a correlation between floating ability and seed longevity. This would imply that in medium-dry environments, species with long-lived seeds may profit from occasional inundations.

WIND

The proportion of species with a high potential for dispersal by wind increases with decreasing nutrient availability and increasing openness of the vegetation structure. At least two complementary mechanisms may explain this relationship. Firstly, the efficiency of wind as a dispersal vector is constrained by the height and density of the surrounding vegetation. Wind can be a very effective long-distance dispersal vector, but is only reliable if the propagules become entrained by turbulence in convective updrafts above the vegetation canopy (Tackenberg 2001; Nathan et al. 2002). Within the vegetation, wind speed is inversely related to vegetation density (Grace 1977; Oke 1987), and neighbouring plants may directly intercept propagules (Green & Johnson 1996). In general, therefore, there is only a chance of effective wind dispersal if propagules are released well above the mean canopy height (Tackenberg et al. 2003). Environments with high nutrient availability and low disturbance intensity (correlated with low light availability at ground level) generally have taller and denser vegetation (e.g. Grime 2001), making it increasingly difficult for individual plants to release their propagules above the mean canopy height.

The increase in anemochory along the light availability gradient is presumably also enhanced indirectly by environmental constraints on seed weight. Although there is a huge seed weight variance within communities, median seed weight increases in shaded environments (Salisbury 1974; Thompson & Hodkinson 1998; Bazzaz et al. 2000). This may well be related to larger seeds having a higher probability of successful germination and early seedling growth under high levels of competition for light (Grime & Jeffrey 1965; Thompson & Baster 1992; Westoby et al. 1996). This advantage is, however, at the expense of the capacity for wind dispersal since, with constant seed morphology, heavy seeds have a lower terminal velocity than light seeds (Augspurger & Franson 1987; Greene & Johnson 1993; Tackenberg 2001).

The combination of these two factors (constraints of nutrient availability on canopy height and seed weight) may, in herbaceous species in productive and shaded environments, lead to a selection pressure against morphological adaptations, such as wings and plumes, for wind dispersal. On a smaller temporal scale, an interesting implication of this trait-environment relationship may be that eutrophication can lead to a decrease in the percentage of wind-dispersed species within local communities. Evidence for this has been provided at the population level for some grassland forbs (Soons & Heil 2002).

MAMMALS

In many plant communities, a large fraction of herbaceous plants have the potential to be dispersed efficiently by large mammals, externally or internally. Variations between communities in the proportion of both epizoochorous and endozoochorous species are mainly explained by variation in light availability (Fig. 5.2C and D), but different sets of species and different morphological adaptations

are involved in each case. The increase in the potential importance of both epizoochory and endozoochory by mammals along the light gradient probably reflects the higher grazing intensity of large mammalian herbivores in open communities due to a better supply of 'high quality' food. Shade-tolerant species generally have leaves with a high level of compounds offering defence against herbivores and pathogens (Coley et al. 1985; Davidson 1993; Reich et al. 1999), and communities dominated by these species are thus less attractive to herbivores. Furthermore, herbivore-specific patterns of habitat use at the landscape level may be involved (e.g. shelter and migration in relation to variation in habitat structure), although this behaviour is probably less clearly related to environmental gradients.

BIRDS

In contrast to endozoochory by mammals, endozoochory by frugivorous birds (ornithochory) is most common in forest and shrub communities. Although ornithochory is a special case of endozoochory, it differs in some important aspects from endozoochory by mammals and is therefore treated separately. The most pronounced difference is the higher degree of specialization in bird-dispersed plant species, which, in temperate regions, include many species with large, fleshy, coloured, nutrient- and sugar-rich fruits. In contrast to tropical regions, such fleshy fruits form only a small fraction of the diet of large mammals (Ridley 1930; Snow & Snow 1988; Willson et al. 1989; Herrera 1995). While the capacity for endozoochory by mammals is constrained by seed weight (not fruit weight), due to the higher probability of small seeds escaping destruction by chewing or by the long digestive tract (Janzen 1984; Pakeman et al. 2002), this is less the case for bird-dispersed seeds with fleshy fruits. Therefore the trade-off between dispersal capacity and recruitment capacity in shaded environments (Thompson & Baster 1992; Westoby et al. 1996) is probably less strong in specialized ornithochorous species with large seeds and fleshy fruits (Herrera 1995; with the exception of extremely large-fruited species, but these are not native in the study area). The higher probability of heavy seeds germinating successfully in shaded environments (Grime & Jeffrey 1965; Westoby et al. 1996) is counterbalanced by the need for large investments of resources in the fruit and selective pressure for the development of fleshy fruits is therefore expected to be strongest in shaded environments.

Multiple dispersal vectors are the rule

THE RELATIVE IMPORTANCE OF HAVING MULTIPLE DISPERSAL VECTORS

If we consider the various dispersal vectors together, the results demonstrate that the ability of species to be dispersed by multiple long-distance dispersal vectors is a common phenomenon in many plant communities. The mean number of potential dispersal vectors per species is greatest in communities with a high light availability (Fig. 5.3). This larger number of potential dispersal vectors does not necessarily mean that dispersal is more effective, but it does at least indicate that, on

average, the species in communities with a high light availability have more opportunities for long-distance dispersal and are thus less dependent on the availability of single dispersal vectors (risk spreading). The results confirm the generalization made by various authors (e.g. Harper et al. 1970; Connell 1978; Grime 2001) that species with a high dispersal ability will prevail in communities with large-scale or high-intensity disturbances, while adaptations for long-distance dispersal will be less common in late successional stages. This generalization rests on the assumption that, in communities with a severe disturbance regime, a selective advantage is gained by those species that succeed in spreading high densities of propagules across large parts of the landscape (Levin et al. 1984; Venable & Brown 1988; Grime 2001).

The increase in the mean number of potential long-distance dispersal vectors per species with increasing light availability is complemented by a decrease in longevity of individual plants (data not shown) and a decrease in the proportion of species with no access to any long-distance dispersal vectors (Fig. 5.2F). This suggests increased importance of investment in attributes favouring the colonization of new sites (long-distance dispersal) relative to short-distance dispersal and local persistence. This notion is consistent with the existence of a trade-off between dispersal ability and adult longevity, as suggested by Shmida & Ellner (1984), Tilman (1994), Ehrlén & Van Groenendael (1998) and Van Groenendael et al. (2000).

DIFFERENCES IN SENSITIVITY TO FRAGMENTATION BETWEEN PLANT COMMUNITIES

The differences between communities in the proportion of species that have access to multiple dispersal vectors probably implies that communities differ in mean rate of long-distance dispersal. These differences may lead to differences in the sensitivity of different plant communities to habitat fragmentation. Moreover, this finding has important consequences for restoration management, because it means that even if the abiotic conditions can be properly restored, communities will probably still differ in the probability of establishment of a representative set of characteristic species from the regional species pool.

It is important to keep in mind that the trait spectra reported here represent only the potential dispersal ability of species. This is no guarantee of actual seed transport, which will be determined by the production of ripe seeds and by the actual availability of dispersal vectors. In the long term, the decline of specific dispersal vectors (e.g. large herbivores) may result in a decline of a subset of species from the regional species pool which depends on these dispersal vectors. This hypothesis, however, remains to be tested. In restoration projects that try to counteract the effects of habitat fragmentation, our results may be used to suggest which dispersal vectors need to be restored when aiming at complete recovery of the 'target communities'.

The effects of habitat fragmentation may be delayed if species with a lower dispersal capacity have higher local persistence, as suggested by Tilman (1994)

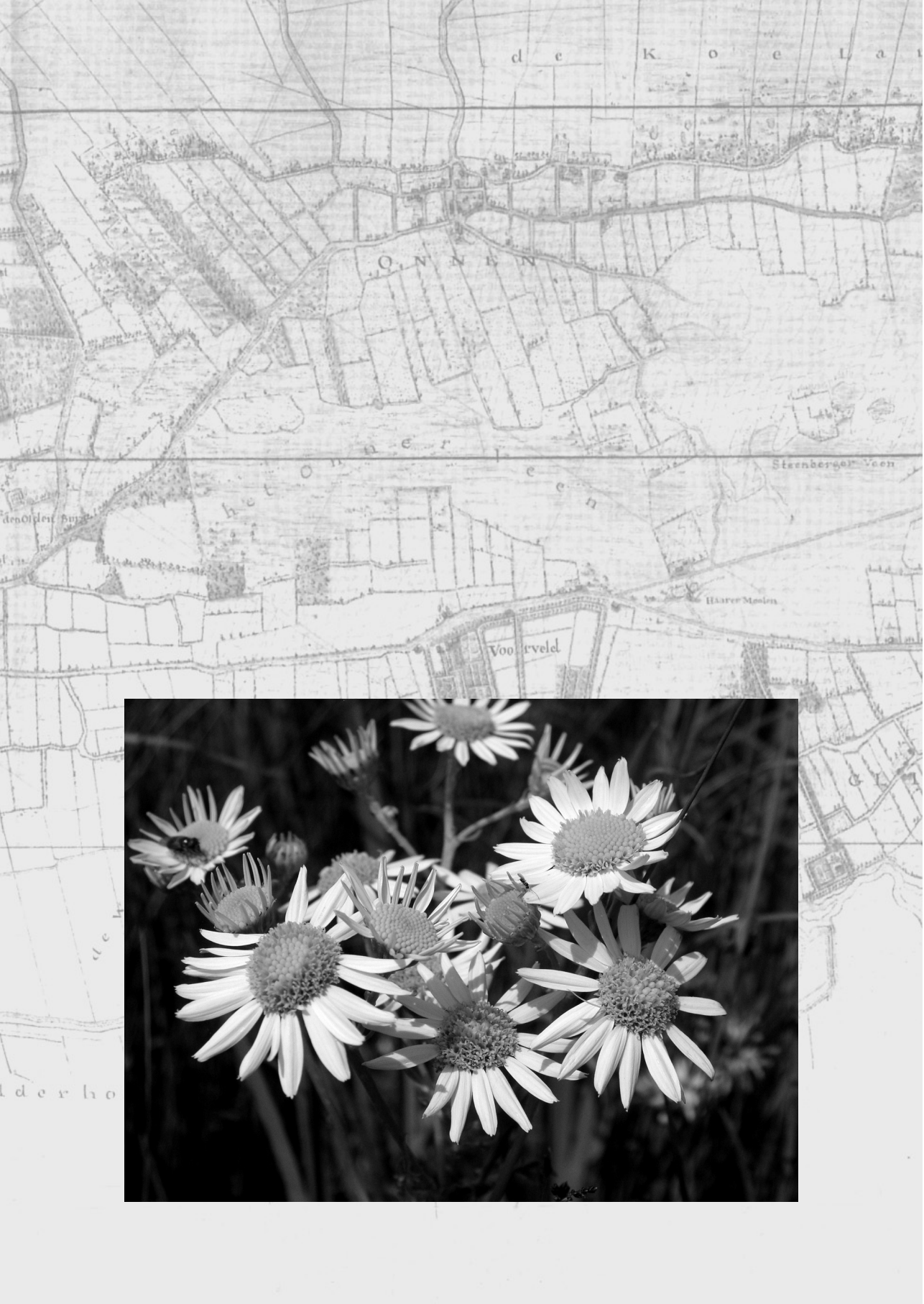
and Ehrlén & Van Groenendael (1998). The buffering effects of high adult persistence cease to be important after severe disturbance or after the creation of new environments.

TOWARDS MULTIPLE VECTOR DISPERSAL MODELS

The observation that, even in relatively stable late-successional communities (e.g. forests), potential dispersal by more than one long-distance dispersal vector is a common phenomenon (Fig. 5.3), sets limits to the applicability of dispersal models. Whereas most existing dispersal models only consider a single dispersal vector (see Nathan & Muller-Landau 2000), our results emphasize the need for 'mixed dispersal models' (e.g. Clark et al. 1998; Higgins & Richardson 1999) based upon multiple dispersal vectors. Furthermore, from the linkages between dispersal traits and environmental conditions, it becomes evident that dispersal models should explicitly include parameters for habitat characteristics in order to integrate niche-based and dispersal-based assembly rules.

Acknowledgements

This research was financially supported by the Netherlands Organization for Scientific Research (NWO-ALW). Stephan Hennekens provided technical assistance. J.P. Bakker, E. van der Maarel, M. Hutchings, and two anonymous referees made valuable comments on an earlier draft of the manuscript and J. Klerkx improved the English.



Assessing the relative importance of dispersal in plant communities using an ecoinformatics approach

Ozinga, W.A., S.M. Hennekens, J.H.J. Schaminée, R.M. Bekker, A. Prinzing, S. Bonn, O. Tackenberg, P. Poschlod, K. Thompson, J.P. Bakker & J.M. van Groenendael (2005).

Folia Geobotanica 40: 53-68.

Marsh Ragwort (*Senecio aquaticus*) is a characteristic species of wet grasslands. Even though the seeds are equipped with a pappus for efficient wind dispersal, it leaves many seemingly suitable habitat patches unoccupied. Its ability for wind dispersal is lower as compared to more ruderal *Senecio* species.

Abstract

Increased insight in the factors that determine the importance of dispersal limitation on species richness and species composition is of paramount importance for conservation and restoration ecology. One way to explore the importance of dispersal limitation is the use of seed-sowing experiments, but it is not feasible to screen large sets of species and habitats. In the present paper we present a complementary approach based on a comparison of small plots with larger regions with regard to species composition and distribution of functional traits. We developed a GIS tool to quantify species pools at various spatial scales, based on ecological and geographical criteria. In this GIS tool large databases are exploited, containing floristic, phytosociological and functional information. Our premise is that differences in the nature of the species in local and regional species pools with regard to functional traits, can give important clues to the processes at work in the assembly of communities.

We illustrate the approach with a case study for mesotrophic hay meadows (*Calthion palustris*). We tested the effects of differences in frequency in the local Habitat Species Pool and differences in dispersal and persistence traits of species on local species composition. Our results show that both species pool effects and functional traits affect the probability of occurrence in small plots. Species with a high propagule weight have, given the frequency in the Local Habitat Species Pool, a lower probability of occurrence in small plots. On the other hand, the probability of local occurrence is increased by the ability to form a persistent soil seed bank and by adult longevity. This provides support for the view that the degree of dispersal limitation is dependent on the degree of spatial isolation of the focal site relative to source populations and moreover that species inherently differ in the degree to which dispersal limitation is a limiting factor for local occurrence.

Introduction

Evidence is accumulating that local species richness and species composition is determined by both niche based processes and dispersal processes (Ricklefs & Schuler 1993, Zobel 1997, Grace 1999, Kupferschmid et al. 2000, Grime 2001, Xiong et al. 2003, Foster et al. 2004, Ozinga et al. 2005). However, the knowledge of the relative importance of both sets of processes under various conditions is fragmentary (Huston 1999, Kolb & Diekmann 2004, Mouquet et al. 2004, Zobel & Kalamees 2005). From a theoretical perspective, this knowledge is important since it touches upon basic principles of community assembly.

Increased insight in the factors that determine the relative importance of various constraints on species richness and species composition is also of paramount importance for conservation and restoration ecology. Growing concern about the decrease of biodiversity at local and regional scales has resulted in increased efforts for restoration of species rich habitats. But even if abiotic conditions can be restored sufficiently, the degree to which characteristic species recolonize the target area is often disappointing (e.g. Hutchings & Booth 1996, Bakker & Berendse 1999, Lockwood & Pimm 1999). It is increasingly acknowledged that the availability of seeds can be a major limiting factor in ecological restoration projects (Bakker & Berendse 1999, Turnbull et al. 2000, Ehrlén & Eriksson 2000, Mouquet et al. 2004). For efficient restoration efforts it is therefore important to have reliable indications to what degree the lack of certain target species might be explained by dispersal limitation or whether other constraints are involved. In other words: it is necessary to differentiate between sites that are unsuitable for the establishment of species from an environmental perspective and sites that are suitable but yet unoccupied (Freckleton & Watkinson 2002, Münzbergová & Herben 2004, Ozinga et al. 2005).

How to test the relative importance of dispersal

Seed addition experiments

One way to explore the relative importance of dispersal limitation is the use of seed-sowing experiments (e.g. Tilman et al. 1997, Turnbull et al. 2000, Zobel et al. 2000, Xiong et al. 2003, Mouquet et al. 2004). If sowing of plant species from the regional species pool results in a sustainable increase in species number at the local scale, we may take this as evidence that species richness is limited by dispersal (Foster & Tilman 2003, Zobel & Kalamees 2005). Seed addition experiments however suffer from several methodological complications (Mouquet et al. 2004, Zobel & Kalamees 2005) and we agree with Zobel & Kalamees that there is a need for well designed, long-term seed addition experiments according to a common design across various ecosystems and geographical regions. However, there is a dilemma between scale and precision. A large scale experiment may differentiate

between alternative hypotheses on the importance of dispersal limitation, but it is not feasible to screen large sets of species and habitats. This is an important drawback from the perspective of restoration ecology, since information on the degree of dispersal limitation is needed for large sets of species and habitats. This dilemma between scale and precision of ecological research may be mitigated by adopting complementary approaches.

Analyses of species richness across spatial scales

Early attempts to deduce the importance of dispersal limitation were based on simple correlations between local and regional species numbers for a given habitat type (e.g. Ricklefs 1987, Cornell 1993, Pärtel et al. 1996, Zobel 2001). The critical issue in these studies was whether (1) local species richness ‘saturates’ at some level independent of the total size of the pool of regionally available species, or (2) local species richness continues to increase as the size of the regional species pool increases. In the first case species richness is considered to be controlled by local interactions, while in the second case local species richness is mainly controlled by regional processes (Cornell 1993, Huston 1999). Using a meta-analysis Cornell & Karlson (1997) and Cornell (1999) showed that unsaturated species-richness curves are the rule, thus supporting the view that dispersal limitation is an important constraint for local species richness.

Correlations between local species richness and the size of the regional species pool, however, cannot exclude the possibility that these relations are simply a passive result of the accumulation of local processes (Rosenzweig & Liv 1999, Herben 2000, Lep 2001, Wilson & Anderson 2001). Moreover this approach may suffer from the inclusion of inappropriate spatial or temporal scales with regard to the processes of interest (Huston 1999). In several studies (e.g. in Cornell & Karlson 1997) for example, the scale of local plots was too large in comparison to the scale at which interspecific interactions take place (Huston 1999, Loreau 2000).

Analyses of species composition and functional traits across spatial scales

A possible way to overcome the methodological problems associated with the comparison of the species numbers across spatial scales may be to shift the focus from species numbers towards the composition and functional attributes of the species concerned. In this paper we propose the usage of such an approach based on the linkage of information available in large databases. Our premise is that differences in the nature of the species in local and regional species pools with regard to functional traits, can give important clues to the processes at work in the assembly of communities. Dispersal limitation is expected to be affected by processes at both the landscape level and the species level.

At the landscape level, the degree of dispersal limitation can be affected by the composition and frequency of species in the species pool, since this determines the availability of propagules.

At the species level there are intrinsic differences in the ability to disperse in space and through time, due to trade-offs between dispersal ability and other life-history traits. Dispersal ability is hypothesised to be negatively related to adult longevity and competitive ability (Grubb et al. 1982, Venable & Brown 1988, Tilman 1994, Ehrlén & Van Groenendael 1998) or to the ability to establish under harsh conditions (Grime & Jeffrey 1965, Westoby et al. 1996, Leishman 1999). In metapopulation theory, the probability of local occurrence of species is described as a dynamic equilibrium between colonization and local extinction (Hanski 1998, Hanski & Gaggiotti 2004). Traits affecting species' dispersal ability and local persistence can be expected to affect this equilibrium (Tilman 1994, Ehrlén & Van Groenendael 1998, Eriksson 2000). The degree of dispersal limitation may therefore be expected to differ between species.

Although the existence of interspecific differences in dispersal traits is well established, this does not necessarily mean that these differences at the species level affect local species composition. This is only the case if dispersal limitation is an important process relative to other processes that determine local species composition such as resource availability and species interactions. Hubbell (2001) even suggests that interspecific differences in traits are not important at all in determining patterns in species regional abundance (frequency). Hubbell (2001) explains abundance patterns solely based on random processes. The critical question is thus not whether species differ in their dispersal ability, but whether these differences translate into differences in the probability of local occurrence. In the present paper we tested the effects of differences in frequency in the species pool (landscape level) and differences in dispersal traits (species level) on local species composition. In the case study we tested the following hypotheses:

Landscape level:

H0: The probability of occurrence of species in small plots is independent of the frequency of species in the species pool

H1: The probability of occurrence of species in small plots increases with frequency in the species pool.

Species level:

H0: No differences exist between species with different functional traits in their probability of occurrence in small plots, given their frequency in the species pool.

H1: Species with a limited ability for dispersal in space, for dispersal through time or with a short adult longevity are underrepresented in small plots, given their frequency in the species pool.

Introduction of an ecoinformatics approach

Outline of the approach

In the present paper we present an approach for the quantification of the relative importance of dispersal limitation based on a comparison of small plots with larger regions with regard to species composition and distribution of functional traits. For this comparison we used large databases containing spatiotemporal explicit data on species composition in small plots ($<100\text{m}^2$) as well as species occurrences in 1 km^2 grid cells. The third component of our approach consists of a species trait database containing information on capacity of species to disperse in space and through time and on adult lifespan. The databases were applied within a Geographic Information System (GIS) to determine the species composition and functional attributes on different spatial scales. The integration of vast ecological databases on different organisational levels and across spatial scales to reveal new information can be regarded as an example of the emerging field of 'ecoinformatics'.

The databases

VEGETATION DATABASE

Co-occurrence data were obtained from the vegetation database of the Netherlands, which comprises over 400,000 specific descriptions of the species composition of small plots (Hennekens & Schaminée 2001, see Box 2 in Chapter 1). It probably is the largest database of local plant species co-occurrence data worldwide to day. The database is based on a large 'space-time window' (plots having been described throughout the Netherlands over the period of 1930 to 2000) and covers a large proportion of the environmental 'niche space' in the Netherlands. Plot size in this database has been scaled approximately according to the mean size of individual plants and ranges from 4 m^2 (grasslands) to 100 m^2 (forests). The position of all plots is recorded within a 1 km^2 grid (and often the exact coordinates as well).

FLORISTIC DATABASES

Floristic data were obtained from the databases FLORIVON and FlorBase. For further details see Van der Meijden et al. (2000) and Tamis & Van 't Zelfde (2003). These databases contain information on species occurrences within 1 km^2 grid cells in the Netherlands in the period 1902-1949 and the period 1975-1999, with 1.7 respectively 4.3 million records. In the present paper we only used the recent floristic data.

TRAIT DATABASE

Data on functional traits of species were extracted from the LEDA database on life-history traits of the species of the Northwest European flora (Knevel et al. 2005, Kleyer et al. in prep.) and adapted to a binary classification (see Chapter 2). We included three groups of traits that are considered to be important for the

spatial and temporal dynamics of species (cf. Tilman 1994, Eriksson 2000, Ehrlén & Van Groenendael 1998, and Muller-Landau et al. 2003): (1) potential for long-distance dispersal, (2) potential to build up a persistent soil seed bank ('dispersal through time'), and (3) adult persistence (see Table 6.1). These three traits are expected to contribute to the predictability of the local occurrence of a particular species, either by fast and frequent re-colonisation of unoccupied sites or by persistence once a re-colonisation has taken place.

For dispersal in space we consider the following dispersal vectors with a high efficiency for long-distance dispersal: water (*hydrochory*), wind (*anemochory*), attachment to the fur of large mammals (*epizoochory by mammals*), survival in the digestive tract of large mammals (*endozoochory by mammals*) and frugivorous birds (*endozoochory by birds*). In order to include as many species as possible and to facilitate comparisons between different dispersal vectors, we aggregated the available data into a binary classification, assigning each species to one of two classes for each dispersal agent: '1' if the species has attributes that give access to a given vector and '0' if the species has no such attributes (see Chapter 2). Although the binary classification of the continuum is less precise for the individual case, it allows generalizations at the level of large species pools. For the classification of dispersal through time we used the seed longevity index (after Bekker et al. 1998, based on data derived from the LEDA database). Species were classified as long-lived if their lifespan exceeds two years.

Table 6.1: Overview of the functional plant traits used in the case study.

Functional trait	Description
GHSP _{Netherlands}	Number of occupied 1 km ² grid cells in the period 1975-1999 (log transformed)
GHSP _{r=3km}	Percentage of occupied 1 km ² grid cells within a radius of 3 km around the focal plot
Propagule weight	Propagule weight (mg; log transformed)
Dispersal potential water	Potential for Long Distance Dispersal by water (0 = low, 1=high)
Dispersal potential wind	Potential for Long Distance Dispersal by wind (0 = low, 1=high)
Dispersal potential fur	Potential for Long Distance Dispersal by fur of mammals (0 = low, 1=high)
Dispersal potential dung	Potential for Long Distance Dispersal by dung of mammals (0 = low, 1=high)
Dispersal potential birds	Potential for Long Distance Dispersal by bird-droppings (0 = low, 1=high)
Seed longevity	Persistence in the soil seed bank (classified with the Seed Longevity Index ranging from 0 = low to 1=high)
Adult longevity	The average length of life of an adult plant (1=annual or biennial, 2=perennial)

The determination of species pools from the databases

In this paper we follow Eriksson (1993) and Zobel (1997) in defining the species pool as a set of species which are potentially capable of coexisting in a certain community. This concept thus implies that for an ecologically relevant estimation of species pools both habitat tolerances (environmental filter) and the spatial distribution (geographical filter) of species must be known (Zobel 1997, Zobel et al. 1998). Within a GIS-environment we developed a ‘species pool tool’ that uses both criteria to quantify the species composition of various species pools from the total species list. A conceptual overview of our approach is given in Fig. 6.1.

ENVIRONMENTAL FILTERS

The assembly of local communities is governed by processes that act like filters to select community members from the broader species pool (e.g. Keddy 1992, Zobel et al. 1998, Grime 2001). Such ecological filters applied to the Total Species Pool (TSP) results in a *Habitat specific Species Pool (HSP)*, sensu Kelt et al. 1995, see Fig. 6.1). HSP’s can be defined using detailed knowledge of the optimal occurrence and tolerances of species along the major environmental gradients (Keddy 1992, Zobel et al. 1998). Alternatively HSP’s can be defined using a hierarchical classification of plant communities (phytosociological approach cf. Zobel et al. 1998, Dupré 2000). This approach builds on the premise that the set of species that are present in a plot has a predictive value for the habitat suitability of that

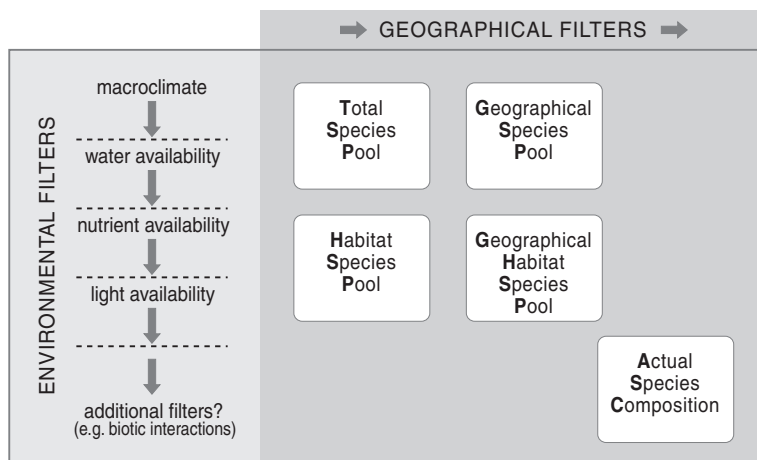


Figure 6.1: Conceptual model of the major constraints on the composition of the actual species composition in small plots, which operate as environmental filters and isolation filters on the Total Species Pool. The Geographical Species Pool can be determined at various spatial scales (e.g. local versus regional sensu Zobel 1997). Terminology for species pools adopted from Kelt et al. 1995, terminology of filters is adapted from Keddy (1992) and Zobel (1997), while the nature of the environmental filters is based on Ozinga et al. (2005).

plot for other species which are not present (cf. McCune 1994, Witte 1998, Ewald 2002). Each individual plots was assigned to one or more vegetation types (maximal three) using the software package ASSOCIA (Van Tongeren et al. 2007). The assignment of each plot is based on the calculated maximum likelihood, using the dissimilarity between a plot and a set of pre-classified reference plots. All species which were observed with a frequency of more than one percent within a plant community were assigned to the HSP of that community. For plots that were identified as transitions between two or three vegetation types we used for each species the average for the frequency values in the vegetation types weighted by the likelihood for the assignment to each vegetation type. The HSP can be regarded as a 'fuzzy set' composed of species with a different degree of community membership and most species belonging to more than one HSP. Note that HSP's are scale independent and constitute habitat defined subsets of the Total Species Pool (TSP).

GEOGRAPHICAL FILTERS

Based on the spatially explicit floristic inventories of 1 km² grid cells in the Netherlands it is possible to quantify the species composition of a *Geographically delimited Species Pool* (**GSP** sensu Kelt et al. 1995) at several spatial scales (Fig. 6.2). On the largest spatial scale the GSP_{Netherlands} equals the Total Species Pool and is defined as the total species list for the Netherlands with their frequencies based on the floristic databases (number of occupied 1 km² grid-cells; Van der Meijden et al. 2000).

At smaller spatial scales it is possible to quantify the species composition in the surroundings of any specific locality in the Netherlands. We used the GIS package ArcView GIS3.2 (© ESRI INC. 1992-1999) to quantify the percentage of occupied 1 km² grid cells in circles around each selected plot at various spatial scales. This results for each plot in a series of local and regional Geographical Species Pools (GSP). The spatial scales can be user defined by specifying the radius around the focal locality.

GEOGRAPHICAL AND ECOLOGICAL FILTERS COMBINED

Since species pools make only sense for sets of species which are potentially capable of coexisting in a certain community, we filter the GSP with the species list from the HSP. This *Geographically delimited Habitat Species Pool* (**GHSP**) is thus the site specific and scale specific intersection of HSP and GSP (e.g. GHSP_{r=3km} = HSP \cap GSP_{r=3km}). GHSP's are unique for each plot for each spatial scale (Fig. 6.2). Higher frequency values in the local and regional GHSP are regarded as indicative for a higher probability of propagule dispersal towards the focal plot, and hence indicate a lower degree of isolation of the focal site. The user defined scale in the GHSP enables a flexible quantification of the composition and frequency distribution of species across spatial scales.

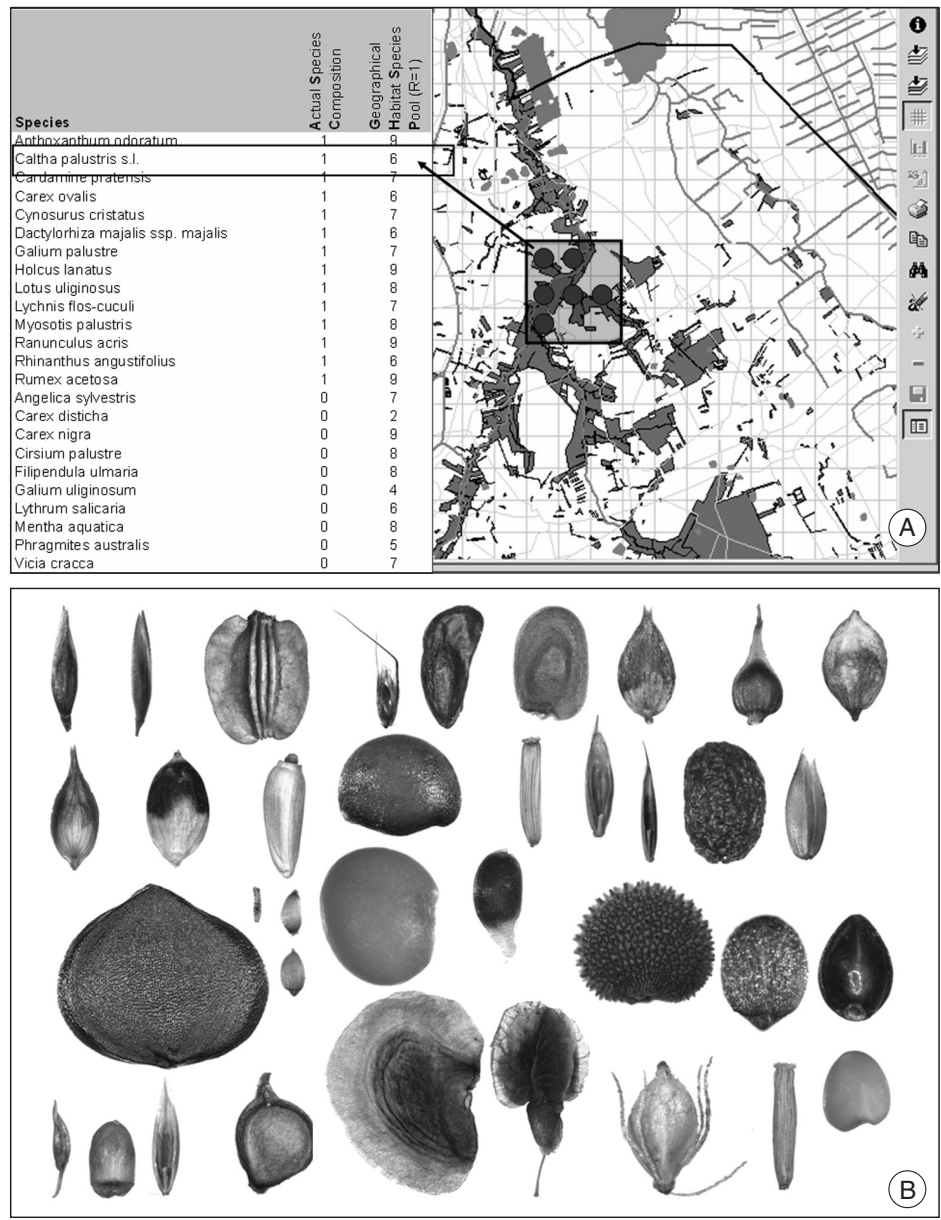


Figure 6.2: Illustration of two steps in the procedure to quantify various species pools. Panel A: GIS-based characterisation of the abundance of species within the Geographical delimited Habitat Species Pools by linking the species composition in individual plots to grid based information on species distributions (in this example the frequency of occurrence of species belonging to the Habitat Species Pool within a radius of 1km: $\text{GHSP}_{R=1\text{km}}$; e.g. *Caltha palustris* occurs in 6 out 9 grid cells). Panel B: The species list from the Habitat Species Pool can be subsequently linked to information on functional traits such as traits associated to seed dispersal (seed photos from Cappers et al. 2006).

Quantification of the relative importance of dispersal: a case study in hay-meadows

Materials and methods

In order to illustrate our approach we present the results of a case study from one plant community. We selected moist mesotrophic hay meadows belonging to the association *Ranunculo-Senecionetum aquatici* (alliance *Calthion palustris*) as described in Schaminée et al. (1995-1999). The ecology of this community is well studied in the Netherlands (e.g. Everts & De Vries 1991, Bakker & Olff 1995, Schaminée et al. 1995-1999, Grootjans et al. 1996, Pegtel et al. 1996). The composition of the Habitat Species Pool (HSP) for this plant community was derived from Schaminée et al. (1995-1999), but the frequency of the constituting species was derived from the floristic database ($\text{GHSP}_{\text{Netherlands}} = \text{HSP} \cap \text{GSP}_{\text{Netherlands}}$).

We used a selection of 500 plots, each with an area of 4m² for which the position within the 1 km²-grid is known. Each 1 km² grid cell was represented maximal by one plot and plots are scattered throughout the Netherlands to reduce confounding effects of spatial autocorrelation. For each plot the actual occurrence of all the species of the $\text{GHSP}_{\text{Netherlands}}$ was scored on a binary scale (present or absent). Subsequently, we determined for each plot the GHSP within a radius of 3 km ($\text{GHSP}_{r=3\text{km}}$). Although the determination of species pool effects across spatial scales is possible with this GIS approach, this is beyond the illustrative scope of the present case study. The ($\text{GHSP}_{r=3\text{km}}$) is based on floristic information from maximal 45 km² grid cells. Plots near the Dutch border were excluded. For the determination of $\text{GHSP}_{r=3\text{km}}$ we only used the recent floristic data. The set of plot specific species pools can now be used to test the hypothesis that frequency in the species pool ($\text{GHSP}_{r=3\text{km}}$) is a good predictor of occurrence in the small plots.

After this, the results can also be linked to the database with functional traits to test for additional effects of functional traits on the probability of occurrence in the 4m² plots. An overview of the functional traits included in the present study is provided in Table 6.1.

STATISTICS

The relative importance of spatial isolation and various functional traits on the probability of occurrence in small plots was quantified by means of multiple logistic regression. This method is based on fewer assumptions than simple linear regression (McCullagh & Nelder 1989) and is considered an effective method in describing binary ecological data (e.g. Austin et al. 1990, Trexler & Travis 1993, Huisman et al. 1993). Although high proportions of unexplained variance are inherent to presence / absence data since the chance of occurrence in specific sites translates into a binary pattern, logistic regression may still provide a powerful tool to separate between alternative hypotheses (Austin et al. 1990, Trexler & Travis 1993). The statistical analyses were performed using SPSS 10 (© SPSS Inc. 1989-1999).

As individual cases we used the occurrence of a given species in a given plot (0 or 1) and associated to this record the percentage of occupied 1 km² grid cells within a radius of 3 km (plot and species specific). The total number of cases was 36295.

In order to test for the effects of species frequency in the local GHSP we need a proper null model based on random dispersal. For a given habitat random dispersal would imply that the species were assigned to plots by a weighted lottery (cf. Chesson & Warner 1981) in which the probability of occurrence in a plot is determined by the frequency in the GHSP_{Netherlands}. Therefore we used a regression model with for each species the percentage of occupied 1 km² grid cells (log transformed) in the Netherlands (GHSP_{Netherlands}) as our null model, and this variable was entered first into the regression model.

We performed the multiple logistic regression in three steps. Firstly, we tested the effect of abundance in the GHSP for the entire Netherlands (GHSP_{Netherlands}). This model was used as our null model. Secondly, we tested for the effect of spatial isolation relative to the null model, and thirdly we tested for additional effects of functional traits. In the third step the functional traits were entered to the model by stepwise forward selection. The parameters of the model were estimated by the likelihood ratio test. This is an assessment of the improvement of the fit between the predicted and observed values on the response variable by adding the predictor variable. Only variables for which the likelihood ratio χ^2 had a P-value <0.05 were included in the model.

Results and discussion

Our test of the hypotheses at the landscape level is presented in Table 6.2 (null model versus species pool effect). The results demonstrate that the frequency of species in the Habitat Species Pool for the entire Netherlands (GHSP_{Netherlands}) explains a significant proportion of the variation in probability of occurrence in small plots. This can be regarded as an effect of random sampling from the GHSP_{Netherlands} according to statistical rules without ecological meaning. This result is consistent with lottery theory (Chesson & Warner 1981) and with neutral theory (Hubbell 2001), in which species are common or rare purely by chance. The proportion of explained variance, however, is very low (Nagelkerke $R^2 = 0.004$) indicating that this cannot be the main explanation for species occurrence patterns, and thus that there must be other mechanisms involved in the assembly of local communities.

The inclusion of spatial differences in the frequency within the local Habitat Species Pool (GHSP_{r=3km}) largely improves the performance of the model (Table 6.2; Nagelkerke $R^2 = 0.190$). The large effect of frequency in GHSP_{r=3km} in explaining the actual occurrence in 4m² plots is consistent with both species pool theory (Eriksson 1993, Zobel 1997) and metapopulation theory (Hanski 1998, Hanski & Gaggiotti 2004). High densities of propagules across the landscape increase the probability of colonization of unoccupied patches. On the other hand can recolonisations of already occupied patches buffer sites against local extinction (Hanski 1998).

Table 6.2: Results of Multiple Logistic Regression with the probability of occurrence in 4m² plots as dependent variable and the frequency of occurrence in the GHSP and functional traits as independent variables. Wald statistics are a measure of the relative effect size of the variables in the full model. Deviations of the odds ratios from 1 indicate the increase in site occupancy with the increase of a given variable. Nagelkerke's R² gives the cumulative proportion of explained variance after entrance of the variable.

Variable	Wald	df	Sig.	Odds ratio	Nagelkerke R ²
Nul odel					
TSP	130.789	1	<0.001	1.182	0.004
Species pool effect					
GHSP _{r=3km}	3285.395	1	<0.001	1.034	0.190
Functional traits					
Propagule weight	88.492	1	<0.001	0.816	0.204
Dispersal potential water	423.169	1	<0.001	0.505	0.215
Dispersal potential birds	92.641	1	<0.001	0.205	0.219
Adult longevity	216.156	1	<0.001	1.639	0.223
Seed longevity	137.216	1	<0.001	1.799	0.227
Dispersal potential fur	87.567	1	<0.001	1.423	0.230
Dispersal potential wind	85.032	1	<0.001	1.447	0.233
Dispersal potential dung	28.308	1	<0.001	0.852	0.234
Constant	3806.911	1	<0.001	0.010	

The results at the species level indicate that the probability of local occurrence, given the frequency in the Local Habitat Species Pool (GHSP_{r=3km}), is affected by functional traits (Table 6.2). The additive effect of functional traits is illustrated in Fig. 6.3 for propagule weight. Species with a high propagule weight have, given the frequency in the Local Habitat Species Pool (GHSP_{r=3km}), a lower probability of occurrence in small plots. This can be explained by a trade-off between seed mass and seed number (Jakobsson & Eriksson 2000, Moles et al. 2004). The lower seed output of larger-seeded species means that they have a lower probability to reach suitable sites. Furthermore the probability of local occurrence is negatively correlated with the ability to disperse with water, mammals (internal) or with birds, although the effect size for these variables was limited. The negative correlations for these dispersal traits may be explained by changes in land use in the Netherlands during the 20th century (Chapter 8). On the other hand, the probability of local occurrence is increased by the ability to form a persistent soil seed bank, by adult longevity and by the ability to disperse by wind or in the fur of mammals. The degree of dispersal limitation, given the frequency in the GHSP, will therefore differ between species according to their functional attributes.

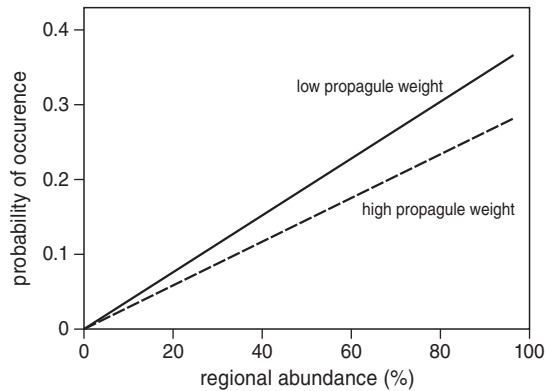


Figure 6.3: Relation between probability of occurrence of a species in a small plot and the frequency of the species in the Geographical delimited Habitat Species Pool (GHSP_{r=3km}) for species with propagule weight <0.3 mg and for species with propagule weight > 0.3 mg. The lines are based on fitted aggregated data (probability of occurrence within abundance classes with an interval of 1%).

Conclusion

Our results indicate that both species pool effects (spatial differences in the frequency of species in the local Habitat Species Pool) and functional traits related to dispersal and local persistence affect the probability of occurrence in small plots. This provides support for the view that degree of dispersal limitation is dependent on the degree of spatial isolation of the focal site relative to source populations and moreover that species inherently differ in the degree to which dispersal is a limiting factor for local occurrence.

These results have important implications for restoration ecology. In highly isolated target areas with an impoverished local Habitat Species Pool (GHSP_{r=3km}) it will not be feasible to re-establish a representative subset of the total Habitat Species Pool (GHSP_{Netherlands}). Characteristic species that are rare in the local GHSP or that lack certain functional traits will be underrepresented in comparison to historical references. This means that either the aims have to be adjusted or alternatively that additional measures are needed, such as reintroduction of species.

Perspectives for the ecoinformatics approach

Our results illustrate that the linkage of databases with spatially explicit data and with functional data within a Geographical Information System can be a powerful tool in the assessment of the relative importance of dispersal limitation. The species pool tool outlined in this paper is however amendable in various ways. In

order to robustly analyse spatial effects the tool should include advanced methods for correction for confounding effects of spatial autocorrelation in environmental conditions (e.g. Legendre et al. 2002). Moreover the species pool tool can be extended by inclusion of spatial explicit information on actual land-use and land-use history. Actual land use may have a large impact on the realized dispersal of propagules from source populations towards target sites. In some habitats past land use may be an even more important predictor of present day species composition (e.g. Poschlod & Bonn 1998, Cousins et al. 2003, Lindborg & Eriksson 2004, Ozinga et al. unpubl. data). This is probably especially true for species with a high adult persistence or with a persistent soil seedbank.

The extension of the ecoinformatics approach critically depends on the availability of ecological data. Since spatial data are often very noisy due to the large role of stochastic events (e.g. Herben & Hara 2003), large phytosociological and floristic databases are required to test hypotheses on community assembly. Moreover the information should be compiled according to common standards (see Mucina et al. 2001, Chytrý 2001, Ewald 2003), and should be spatially and temporally explicit. The phytosociological databases should be compatible with floristic databases and trait databases with regard to database structure and taxonomy to enable the determination of habitat species pools at various spatial scales. The fast increase in availability of ecological databases holds a promise for the near future. Once these databases are sufficiently filled the ecoinformatics approach presented here may provide a useful tool for the further analyses of hypotheses regarding factors that influence the degree of dispersal limitation.



How important is long-distance seed dispersal by wind for regional survival of plant species?

Soons, M.B. & W.A. Ozinga (2005).

Diversity and Distributions 11: 165-172.

Meadow Thistle (*Cirsium dissectum*) is an endangered species of moist, nutrient poor hay-meadows. Although its seeds are equipped with a pappus that facilitates wind dispersal, the vast majority of the seeds (>99%) is dispersed within a radius of 10m. For the common Creeping Thistle (*Cirsium arvense*) in contrast, the falling velocity of the seeds is stronger reduced by the pappus and 1% of the seeds reach distances over 50m.

Abstract

Long-distance seed dispersal is generally assumed to be important for the regional survival of plant species. In this study we quantified the importance of long-distance seed dispersal for regional survival of plant species using wind dispersal as an example. We did this using a new approach, by first relating plant species' dispersal traits to seed dispersal kernels and then relating the kernels to regional survival of the species. We used a recently developed and tested mechanistic seed dispersal model to calculate dispersal kernels from dispersal traits. We used data on 190 plant species and calculated their regional survival in two ways, using species distribution data from 36,800 1 km²-grid cells and 10,754 small plots covering The Netherlands during the largest part of the 20th century. We carried out correlation analyses and stepwise multiple regression analyses to quantify the importance of long-distance dispersal, expressed as the 99-percentile dispersal distance of the dispersal kernels, relative to the importance of median-distance dispersal and other plant traits that are likely to contribute to the explanation of regional survival: plant longevity (annual, biennial, perennial), seed longevity and plant nutrient requirement. Results show that long-distance dispersal plays a role in determining regional survival, and is more important than median-distance dispersal and plant longevity. However, long-distance dispersal by wind explains only 1–3% of the variation in regional survival between species and is equally important as seed longevity and much less important than nutrient requirement. In changing landscapes such as in The Netherlands, where large-scale eutrophication and habitat destruction took place in the 20th century, plant traits indicating ability to grow under the changed, increasingly-nutrient-rich conditions turn out to be more important for regional survival than the ability for seed dispersal by wind.

Introduction

Many plant species have morphological traits to enhance dispersal of their seeds by specific vectors. These traits are considered to be adaptations to dispersal over specific ranges of distances and/or to specific micro-sites, which benefits species survival through (1) escape from kin-competition, predators and pathogens and (2) colonization of unoccupied habitat patches (Howe & Smallwood 1982; Nathan & Muller-Landau 2000; Willson & Traveset 2000). Species with traits that enhance long-distance seed dispersal (e.g. a pappus that enhances seed dispersal by wind) usually disperse the majority of their seeds over - somewhat - longer distances than other species, but disperse a small number of their seeds over very long distances (Soons et al. 2004b). The few seeds that disperse over long distances make up the rare long-distance dispersal (LDD) events that are considered an important component of the survival strategy of such species.

Theoretical studies have demonstrated that LDD enhances species range expansion and migration (e.g. Higgins et al. 1996; Higgins & Richardson 1999; Kot et al. 1996; Clark 1998). Theoretical studies also demonstrated that LDD enhances regional survival of species in dynamic landscapes, especially landscapes with high turnover of habitat patches or habitat fragmentation (e.g. Malanson & Armstrong 1996; Valverde & Silvertown 1997; Hanski 1998, 1999). The positive effect on regional survival is based on the assumptions that (1) LDD increases the frequency and speed of colonization of unoccupied habitat patches and (2) LDD increases gene flow between occupied habitat patches so that the probability of extinction in these patches is reduced. Geographical range studies and studies on plant migration have provided evidence that LDD occurs and enhances plant range expansion and migration (e.g. Macdonald 1993; Pitelka et al. 1997; Cain et al. 1998; Petit et al. 2002). Empirical studies have related basic plant traits such as seed mass to species distributions and changes in distributions (Thompson 1994; Thompson et al. 1999; Kahmen & Poschold 2004; Ozinga et al. 2005). However, no empirical studies have been able to link morphological plant traits that indicate LDD by a specific dispersal vector to (1) actual ability for LDD and (2) regional survival of plant species. This is partly because ecologists are only starting to establish quantitative relationships between plant traits and dispersal distances including LDD (for wind dispersal most progress has been made, see Nathan et al. 2002; Soons et al. 2004a; Nathan et al. 2005). It is also partly because the analyses needed to test for such links require detailed data on plant traits and plant distributions of a large number of species, which until now were not readily available.

The aim of this study is to quantify the importance of LDD for regional species survival. We do this using a new approach: We first relate plant species' dispersal traits to seed dispersal kernels and then relate these kernels to regional survival of the species. This approach could not be used before, because no tools were available to relate plant traits to realistic seed dispersal kernels including LDD. We use a recently developed and tested mechanistic seed dispersal model (Nathan et al.

2002; Soons et al. 2004a, 2004b) for this purpose. Also, detailed data on plant traits and distributions of many species were until now not readily available. We use data from large databases that are currently being made available to ecologists in digital form. This allows us to include data on many plant species and their distributions and makes our results robust. Other advantages of our approach are: First, we can directly quantify the link between LDD and regional survival, without having to use various single estimators of ability for LDD (such as seed terminal velocity and release height) in our analysis. Second, we can distinguish between the importance of rare LDD events in the tail of the dispersal kernel and the importance of overall, or median, dispersal distances. To quantify the relative importance of LDD for regional species survival we also include other plant traits that are likely to contribute to the explanation of regional survival in our analysis: plant longevity, seed longevity and plant nutrient requirement (Tilman 1994; Thompson 1994; Thompson et al. 1999; Ozinga et al. 2005).

Methods

We selected seed dispersal by wind as dispersal mechanism for our study. We chose wind dispersal as example for other dispersal mechanisms, because quantitative relationships that have been established between plant traits and dispersal distances - including LDD - are currently more realistic for wind dispersal than for other dispersal mechanisms (cf. Nathan et al. 2002; Soons et al. 2004a). Also, wind dispersal is a very common dispersal mechanism, making it a general and global example. We selected 190 wind-dispersed plant species of open to relatively open vegetation types in northwest Europe (see Electronic Appendix S1 and S2). Selection criteria were: (1) Occurrence in the selected vegetation types, (2) presence of morphological adaptations to reduce falling velocity (pappus, balloon-like structure or wing-like structure > 0.1 times achene length) or to eject seeds from capsules during wind movement, and (3) data on seed terminal velocity and release height available. We studied regional survival of these species in The Netherlands, a suitable study area for our analysis because species distributions have been well-documented for a long time period (almost the entire 20th century).

To quantify the importance of LDD and the other plant traits (median dispersal distance, plant longevity, seed longevity and plant nutrient requirement) for regional survival we carried out correlation analyses between the plant traits and regional survival. To quantify the relative importance of the plant traits in explaining regional survival we carried out stepwise multiple regression analyses with all traits as independent variables and regional survival as dependent variable. We quantified ability for LDD as the 99-percentile dispersal distance of the seed dispersal kernel of a species. Similarly, we quantified median dispersal distance as the median distance of the dispersal kernel. Dispersal kernels were obtained from simulations with a mechanistic model (see *Simulation of dispersal kernels*). We in-

cluded median dispersal in our analysis to separate the importance of rare LDD events from the importance of 'bulk' dispersal, which is usually over relatively short distances. We quantified plant longevity using life history strategy categories (annual=1, biennial=2, perennial=3), seed longevity in the seed bank (Thompson et al. 1997) using the seed longevity index of Bekker et al. (1998), and nutrient requirement using Ellenberg indicator values for nitrogen (Ellenberg et al. 1992). These data were derived from the LEDA database (<http://www.leda-traitbase.org>). We quantified regional survival using species distribution data at two different scales: Nation-wide 1 km²-grid data and small-scale plot data.

1 Km²-grid data

First, we used frequencies of occurrence of species in 1 km² grid cells covering all terrestrial area of The Netherlands. We used frequency classes from Tamis & Van 't Zelfde (2003) in which several forms of recording bias were eliminated. We used frequency classes for the time periods 1902-1949 ('previous frequency of occurrence') and 1988-1999 ('current frequency of occurrence') and quantified species survival as the change in frequency of occurrence between the two periods. The frequency classes are on a ³log scale, so we transformed them back to linear scale before subtraction and then transformed the absolute differences to ³log scale again, afterwards adding the sign of the difference. These data give a good overview of the survival of plant species in The Netherlands. A limitation is, however, that changes in occurrence of species may result simply from changes in the total area of their habitat in The Netherlands, i.e. from changes in the number of grid cells in which their habitat occurs.

Small-scale plot data

Second, we used frequencies of occurrence of species in small-scale (1–10 m²) plots of specific habitat types in The Netherlands. For this we obtained data from the Dutch Vegetation Database, which comprises >35,000 descriptions of species composition in small plots (relevés) throughout the Netherlands from 1930-1999 (Hennekens & Schaminée 2001, see Box 2). For our analysis we selected 11 vegetation types (see Electronic Appendix S1) using the following selection criteria: (1) Representative of (semi-)natural, open to relatively open vegetation types in The Netherlands, (2) sufficient data available (>100 plots for both time periods), and (3) area of plots approximately equal for both time periods. We again quantified regional survival as the change in frequency of occurrence between two time periods: 1930–1975 ('previous frequency of occurrence') and 1975–1999 ('current frequency of occurrence'). This measure of survival is not a measure of nation-wide survival, but of survival in a specific habitat in which changes in the occurrence of species caused purely by changes in the total nation-wide area of their habitat do not play a role. Effects of the spatial pattern of their habitat and processes such as (re-)colonization of habitat patches and gene flow between habitat patches do however play a role in these data.

Simulation of dispersal kernels

For the calculation of dispersal kernels we assumed that seeds of the selected species are dispersed by wind only and that there is no secondary dispersal. We calculated dispersal kernels from plant traits using a mechanistic seed dispersal model: the Synthetic Turbulence Generation Markov chain model (Soons et al. 2004a). This model is a slightly modified version, adapted for wind dispersal in relatively open ecosystems, of a model previously developed by Nathan et al. (2002). The model simulates dispersal trajectories of individual seeds as determined by gravity, air resistance and wind flow, including wind turbulence. The main difference between this model and other mechanistic dispersal models (e.g. Andersen 1991, Tackenberg 2003) is its simulation of realistic wind turbulence and hence realistic LDD (Nathan et al. 2002; Soons et al. 2004a, 2004b). The simulated wind turbulence is stochastic, so that seeds experience unique dispersal trajectories. For each species we simulated 10,000 dispersal trajectories to create a dispersal kernel.

The model uses two plant traits as input parameters: seed terminal velocity and release height. We obtained species' mean terminal velocity and mean release height from the LEDA database (<http://www.leda-traitbase.org>; see also Chapter 2). A third plant trait, period of seed release, determines the model wind velocity input. We estimated the two-month period during which each species' seed release peaks from Bouman et al. (2000). For each two-month period of the year we used the natural distribution of horizontal wind velocities in The Netherlands as wind velocity input (wind velocity distributions from Wieringa & Rijkoort 1983; averages for The Netherlands excluding the coast). The model also uses height and Leaf Area Index (LAI) of the vegetation as input parameters. Vegetation height is the height of the dense part of the vegetation, i.e. excluding flowering stalks. Because all selected species occur in the same open and relatively open vegetation types and for practical reasons, we set the vegetation height to 2/3 of seed release height and calculated the wind flow inside and above the vegetation using the median vegetation height (0.35 m, data from the Dutch Vegetation Database) and a standard LAI (3.5). This assumption is realistic for the majority of species because the vegetation types in which they occur have similar heights, but overestimates dispersal distances for tall species that may occur in monospecific tall stands (e.g. *Typha*). For model details and model reliability we refer to Nathan et al. (2002) and Soons et al. (2004a, 2004b).

Statistical analyses

We carried out statistical analyses in SPSS 10 (SPSS Inc. 1989–1999). We used Spearman's correlation coefficient for the correlation analyses, because most data were not normally distributed. In the stepwise multiple regression analyses we excluded species for which any independent variable was missing. Regression models were tested for normality of unstandardized residuals and if necessary the dependent variables were transformed. To get more insight in the relationships

between the independent variables and regional survival we also carried out correlation and regression analyses for the frequencies of occurrence in both time periods. In the analyses for regional survival and current frequency of occurrence we added previous frequency of occurrence as independent variable.

Results

Several of the independent variables in our analyses were correlated (Table 7.1). As expected model output, simulated LDD and median-distance dispersal were almost fully correlated using Spearman's correlation coefficient. Dispersal distance was also correlated with nutrient requirement and plant longevity: The plant species with an optimal occurrence under nutrient-rich conditions and perennial species disperse their seeds over longer distances than the plant species with an optimal occurrence under nutrient-poor conditions and annuals. There was however also a weaker, but significant, negative correlation between nutrient requirement and plant longevity. Seed longevity was positively correlated to nutrient requirement, indicating that the species with an optimal occurrence under nutrient-rich conditions have longer-lived seed banks. Seed longevity was negatively correlated to plant longevity.

Results for the 1 km²-grid data

Results of the analyses are presented in Table 7.2. Frequency of occurrence of the selected plant species in the period 1902–1949 was correlated to plant nutrient requirement, but could not be explained by any of the independent variables used in our analysis. Frequency of occurrence in the period 1988–1999 was correlated with nutrient requirement, seed longevity, LDD and median-distance dispersal. However, by far the highest correlation was with frequency of occurrence in the previous time period. The regression analysis showed that previous frequency of occurrence, nutrient requirement, seed longevity and LDD contribute to explaining

Table 7.1: Correlations between LDD, median distance dispersal, plant longevity, seed longevity and nutrient requirement. For each variable N=190, except for nutrient requirement (N=170) and seed longevity (N=124). * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Spearman's rho	Median dispersal	Nutrient requirement	Plant longevity	Seed longevity
LDD	0.995 ***	0.24 **	0.27 ***	NS
Median dispersal		0.26 **	0.28 ***	NS
Nutrient requirement			-0.19 *	0.27 **
Plant longevity				-0.48 ***

Table 7.2: Results of the analysis of the 1 km²-grid data. Correlation analyses show which variables are related to frequency of occurrence and regional survival of species. Spearman's rho is the correlation coefficient. Stepwise multiple regression analyses show which independent variables best explain frequency of occurrence and regional survival of species. (+) Indicates a positive relationship, (–) a negative relationship. R² values indicate percentage of variation explained. R² values are given for individual variables and full models. Dispersal distances were log-transformed for the analysis. Frequencies of occurrence and regional survival were arctan-transformed for the regression analyses. + p<0.10, * p<0.05, ** p<0.01, *** p<0.001.

Correlating variables		Spearman's rho	Explaining variables in stepwise multiple regression		R ²
Frequency in period 1 (1902-1949)	(+) Nutrient requirem. +	0.13	–		
Frequency in period 2 (1988-1999)	(+) Freq. period 1 ***	0.80	(+) Freq. period 1 ***		0.66
	(+) Nutrient requirem. ***	0.40	(+) Nutrient requirem. ***		0.08
	(+) Seed longevity +	0.15	(+) Seed longevity ***		0.04
	(+) LDD +	0.14	(+) LDD *		0.01
	(+) Median distance +	0.13	Total		0.79
Regional survival: change in frequency from period 1 to period 2	(+) Nutrient requirem. ***	0.49	(+) Nutrient requirem. ***		0.24
	(+) Seed longevity ***	0.39	(+) Seed longevity ***		0.08
	(+) LDD **	0.23	(+) LDD *		0.03
	(+) Median distance **	0.23	Total		0.35
	(–) Plant longevity *	–0.18			

the variation in current frequency of occurrence. Together they explained 79% of the variation, of which only 13% was explained by the plant traits. Regional survival was correlated to all plant traits included in the analysis. The regression analysis showed that three independent variables contribute significantly to explaining the variation in survival: nutrient requirement, seed longevity and LDD.

Results for the small-scale plot data

Results of the analyses for all vegetation types together are presented in Table 7.3. Again, frequency of occurrence of the selected plant species in the first time period (1930–1975) could not be explained by any of the independent variables in our analysis. Frequency of occurrence in the period 1975–1999 was highly correlated with frequency of occurrence in the previous period and also with nutrient requirement, LDD and median-distance dispersal. The regression analysis showed that current frequency of occurrence is explained best by previous frequency of occurrence and for a small part also by nutrient requirement. Regional survival was correlated to all independent variables except plant longevity. The regression

Table 7.3: Results of the analysis of the small-scale plot data when all vegetation types are analysed together. Correlation analyses show which variables are related to frequency of occurrence and regional survival of species. Spearman's rho is the correlation coefficient. Stepwise multiple regression analyses show which independent variables best explain frequency of occurrence and regional survival of species. (+) Indicates a positive relationship, (–) a negative relationship. R^2 values indicate percentage of variation explained. R^2 values are given for individual variables and full models. Dispersal distances were log-transformed for the analysis. Frequencies of occurrence and regional survival were arctan-transformed for the regression analyses. + $p < 0.10$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Correlating variables		Spearman's rho	Explaining variables in stepwise multiple regression	R^2
Frequency in period 1 (1902-1949)	(+) Seed longevity **	–0.13	–	
	(+) Plant longevity +	0.07		
Frequency in period 2 (1988-1999)	(+) Freq. period 1 ***	0.63	(+) Freq. period 1 ***	0.55
	(+) Nutrient requirem. ***	0.17	(+) Nutrient requirem. ***	0.03
	(+) Median distance *	0.08	Total	0.58
	(+) LDD *	0.07		
Regional survival: change in frequency from period 1 to period 2	(–) Freq. period 1 ***	–0.35	(–) Freq. period 1 ***	0.08
	(+) Nutrient requirem. ***	0.25	(+) Nutrient requirem. ***	0.06
	(+) LDD ***	0.12	(+) LDD *	0.01
	(+) Median distance **	0.12	Total	0.15
	(+) Seed longevity *	0.08		

analysis showed that survival could be explained by previous frequency of occurrence, nutrient requirement and LDD. However, the total explaining power of these three variables was relatively low (15%).

Results of the analyses for the vegetation types separately are presented in Table 7.4. Because in all vegetation types specific sets of species occur, relationships of regional survival and frequency of occurrence with plant traits differed between vegetation types. Frequency of occurrence in the first time period was explained by nutrient requirement, LDD and seed and plant longevity. Current frequency of occurrence was explained best by previous frequency of occurrence, followed by nutrient requirement and LDD. R^2 values of the full regression models for frequency of occurrence in 1930-1975 ranged from 0.06-0.33 and were much lower than for frequency of occurrence in 1975-1999 (0.36-0.76). Note, however, that the models for 1975-1999 included an extra explanatory variable. Regional survival was explained best by previous frequency of occurrence, nutrient requirement, seed longevity and dispersal (both LDD and median-distance dispersal). Interestingly, the relationship with previous frequency of occurrence was always

Table 7.4: Results of the stepwise multiple regression analyses of the small-scale plot data when all vegetation types are analysed separately. Results show which independent variables best explain frequency of occurrence and regional survival of species. Per independent variable the number of vegetation types (out of 11) for which the variable is significant ($p < 0.05$) is indicated. Dispersal distances were log-transformed and frequencies of occurrence and regional survival were arctan-transformed for the analyses. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

	Explaining variables in multiple regression	Number of veg. types
Frequency in period 1 (1930-1975)	Nutrient requirem. * - ***	7
	Seed longevity **	2
	LDD * - **	2
	Plant longevity * - **	2
Frequency in period 2 (1975-1999)	Freq. period 1 ***	10
	Nutrient requirem. * - ***	5
	LDD * - **	2
Regional survival: change in frequency from period 1 to period 2	Freq. period 1 ** - ***	7
	Nutrient requirem. ** - ***	4
	Seed longevity *	3
	Median distance * - **	2
	LDD **	1

negative, as in the analysis for all vegetation types together. This indicates that many species that previously were common decreased in abundance, whereas a group of species that was rare in the selected vegetation types (but not so rare elsewhere in The Netherlands) increased in abundance. This corresponds to the finding that previous frequency of occurrence was most often negatively related to nutrient requirement, whereas current frequency of occurrence was always positively related to nutrient requirement. This indicates that in several vegetation types a shift occurred from species with an optimum at nutrient-poor conditions to species with an optimum at more nutrient-rich conditions. R^2 values of the full regression models for survival ranged from 0.15-0.89.

Discussion and conclusions

We quantified the importance of LDD for the regional survival of wind-dispersed plant species in The Netherlands. We used a new approach, by first linking plant traits to ability for LDD and then linking ability for LDD to regional survival. The main advantage of this approach is that realistic, consistent, quantitative measures of species' ability for LDD are related to their regional survival. It should be kept in mind, however, that the quantification of LDD is based on several key as-

sumptions (including dispersal by wind exclusively and equal vegetation height and LAI for all vegetation types) and simulated LDD is an indication, not the exact value, of actual LDD. We used data on 190 plant species and species distribution data for >36,000 1 km²-grid cells and >10,000 small plots, spanning the largest part of the 20th century. These large numbers, the nation-wide coverage of our data and the good agreement between results from different analyses make our results robust. Our results give implications for species conservation; see Trakhtenbrot et al. (2005).

LDD of plant seeds plays a role in determining regional survival of the plant species. LDD is more important than median-distance dispersal: The large differences in ability for LDD between species explain differences in regional survival better than the much smaller differences in median-distance dispersal. LDD is also more important in explaining regional survival than plant longevity. However, the explaining power of LDD is not very great: Ability for LDD explains only ca. 1–3% of the variation in survival. This is comparable to seed longevity, but much less than nutrient requirement, which by far explains the variation in survival best (by 6–24%). Patterns for the explanation of current frequency of occurrence by plant traits are similar to those for regional species survival. Current frequency of occurrence is, however, by far best explained by previous frequency of occurrence (by 55–66%). Previous frequency of occurrence cannot be explained by any of the plant traits when all vegetation types are analysed together, but within vegetation types some plant traits do explain frequency of occurrence. The vegetation-specific results are likely caused by interactions between environmental conditions and plant traits (Ozinga et al. 2004; chapter 5).

Several explanations may contribute to our finding that LDD is of relatively little importance for regional species survival in comparison to nutrient requirement. First, the positive correlation between nutrient requirement and ability for LDD, as well as seed longevity, may have obscured the relationships between survival and LDD and seed longevity in the stepwise multiple regression analyses. However, in the correlation analyses the relationship between survival and nutrient requirement was also much stronger than the relationships between survival and LDD and seed longevity. Second, the assumption that LDD enhances regional survival by increasing the frequency and speed of colonization of unoccupied habitat patches may be wrong. Not necessarily because dispersal distances are too low (in some species 99-percentile dispersal distances were very long; see Electronic Appendix S2), but because during the 20th century many (semi-)natural vegetation types in The Netherlands were destroyed or severely fragmented (Vos & Zonneveld 1993; Soons 2003) and only very few new, suitable but unoccupied habitat patches came into existence. Lack of unoccupied habitat patches reduces the positive effect of LDD on regional survival through increased colonization. Third, the assumption that LDD enhances regional survival by increasing gene flow between occupied habitat patches, so that the probability of extinction in these patches decreases, may be wrong. If habitat destruction and fragmenta-

tion resulted in isolation of all remaining populations (e.g. Soons 2003), LDD does not reduce patch extinction because it does not increase gene flow anymore. This is not very likely though, because several of the selected vegetation types are still relatively common and some species have very long dispersal distances (see Electronic Appendix S2). It is more likely that isolated populations have not suffered from lack of gene flow and a positive effect of gene flow on regional survival is not (yet) discernible. Fourth, the assumption that the selected plant species achieve LDD primarily through primary wind dispersal may have been wrong. Seeds of many plant species have adaptations for dispersal by more than one potential LDD vector (Ozinga et al. 2004, see Chapter 2) or may be dispersed over long distances by nonstandard processes, including secondary dispersal (Higgins et al. 2003). If the selected plant species achieve LDD through a range of different mechanisms, the importance of LDD by wind may be obscured, even though it may be important for regional survival (cf. Hodkinson & Thompson 1997). Fifth, and most likely, is the explanation that habitat requirements are simply much more important for regional survival in The Netherlands than dispersal ability. During the 20th century all vegetation types in The Netherlands experienced changes in abiotic conditions, most notably nitrogen enrichment due to intensification of agriculture (Bobbink et al. 1998; Vos & Zonneveld 1993; Aerts & Bobbink 1999). In many vegetation types this resulted in shifts from species with an optimum at nutrient-poor conditions to species with an optimum at more nutrient-rich conditions (Bobbink 1991; Bobbink et al. 1998; Aerts & Bobbink 1999), as we also found. Results indicating that species with high competitive ability under nutrient-rich conditions are currently increasing most in The Netherlands and other countries with high nutrient emissions have also been found by Thompson (1994), Schaminée et al. (2002) and Tamis et al. (2004).

Finally, the relatively low total amount of variation in regional survival that is explained (15–35%, up to 89% for the vegetation types separately) indicates that other plant traits and/or random processes are also very important. Pollen dispersal distance, success of self-fertilisation and ability to grow under increasingly common environmental conditions other than high nitrogen availability (e.g. tolerance to low groundwater levels) may contribute to the explanation of survival. Detailed quantitative data on these plant traits were not available for our analysis, but are being collected and will be available for future analyses which may find a higher amount of variation in survival explained by plant traits. Alternatively, such future analyses may find that random processes (cf. Hubbell 2001) have a relatively great importance for regional species survival.

We conclude that plant species' ability for LDD by wind is important for their survival in The Netherlands. Ability for LDD by wind is approximately of the same importance as seed longevity in the seed bank. However, under the increasingly nutrient-rich environmental conditions in The Netherlands the ability of species to grow and survive under nutrient-rich conditions is far more important for their regional survival than their ability for LDD.

Acknowledgements

We thank Jan van Groenendael and four reviewers for their comments on earlier versions of this paper.

Supplementary material

The following material is available from

<http://www.blackwellpublishing.com/products/journals/suppmat/DDI/DDI148/DDI148sm.htm>

Appendix S1. Overview of the vegetation types included in the analysis.

Appendix S2. List of plant species selected for the analysis.



Availability of dispersal vectors as a key to plant losses in NW Europe

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At the landscape level, the vectors that transport seeds between sites act like a complex ‘dispersal infrastructure’. During the 19th and 20th century this dispersal infrastructure was strongly impoverished in most parts of Northwest Europe. The exchange of large mammals between sites by free-ranging or herded livestock grazing, for example, has become rare. Among the Northwest European mammals, sheep have the highest capacity for the long-distance transport of seeds by their fur.

Abstract

The ongoing decline of many plant species in Northwest Europe indicates that traditional conservation measures, although useful, are not enough to halt diversity losses. Using recent databases, we show for the first time that differences between species in adaptations to various dispersal vectors, in combination with changes in the availability of these vectors, contribute significantly to explaining losses in plant diversity in Northwest Europe in the 20th century. Species with water- or fur-assisted dispersal are over-represented among declining species, while others (wind- or bird-assisted dispersal) are under-represented. Our analysis indicates that the 'colonization deficit' due to a degraded dispersal infrastructure is no less important in explaining plant diversity losses than that due to eutrophication and associated niche-based processes. Present-day species losses are thus the legacy of changes in the dispersal infrastructure. Our findings call for measures that aim to restore the dispersal infrastructure across entire regions and which go beyond current conservation practices.

Introduction

Understanding the mechanisms behind observed losses of biological diversity is a major scientific challenge for the 21st century (Baillie et al. 2004, Balmford et al. 2005, Millennium Ecosystem Assessment 2005). Changes in plant species composition of vegetations in man-made landscapes are often explained in terms of habitat degradation, especially by eutrophication (Vitousek et al. 1997; Bobbink et al. 1998; Grime 2001; Tilman et al. 2002; Stevens et al. 2004; Suding et al. 2005). Restoration of habitat quality, however, often fails to deliver the expected plant diversity (Dobson et al. 1997; Bakker & Berendse 1999). It has therefore been questioned during the past decade to what extent community composition indeed is constrained by local habitat quality or whether regional processes such as limited rates of seed dispersal are crucial (Hodgson & Grime 1990; Tilman 1997; Poschlod & Bonn 1998; Turnbull et al. 2000; Foster et al. 2004; Ozinga et al. 2005; Mouquet et al. 2004).

Metapopulation theory asserts that regional survival of species requires that local populations are connected by sufficient rates of dispersal (Hanski 1998). The newly emerging concept of 'metacommunities' extends metapopulation theory towards the community level and analyses the role of species specific traits that are important for local and regional processes (Leibold et al. 2004).

In contrast to mobile animal species, plants depend for the transport of their seeds on external vectors, including water, wind, birds and large mammals, each with their own characteristics. At the landscape level, these dispersal vectors act like a complex 'dispersal infrastructure' (cf. Poschlod & Bonn 1998). Although changes in the relative availability of dispersal vectors during the 20th century have been documented in many parts of the industrialized world (Ridley 1930; Beaufoy et al. 1994; Dynesius & Nilsson 1994; Bignal & McCracken 1996; European Environment Agency 2003; see Poschlod & Bonn 1998 for a review), their impact on plant diversity has never been examined in large-scale studies. Dispersal by water has been restricted by the regulation of the natural flood regimes of rivers and brooks for the purpose of flood control, while dispersal by large mammals has declined due to the change from livestock grazing on common grounds to grazing in fenced fields or livestock housing. In Northwest Europe, these changes in dispersal infrastructure mostly took place some 50 to 150 years ago (Ridley 1930; Beaufoy et al. 1994; Dynesius & Nilsson 1994; Bignal & McCracken 1996; Poschlod & Bonn 1998; European Environment Agency 2003; see Box 3).

The potential effect of changes in the availability of dispersal vectors on species losses is founded upon two premises. Firstly, vascular plant species have different specializations in terms of the kind of dispersal vectors which can effectively transport their seeds (known as 'dispersal syndromes' (Ridley 1930; Poschlod & Bonn 1998; Ozinga et al. 2004). Secondly, in any terrestrial habitat, a variety of dispersal vectors may be available, so plants with different dispersal

syndromes may find their requirements satisfied (Ozinga et al. 2004). A decline in the availability of specific dispersal vectors is then expected to result in a decline of those species that, given their traits, depend on these vectors. The effect of limited availability of dispersal vectors on plant diversity has never been tested on large spatial and temporal scales, due to a lack of suitable data.

Methods

Approach

We combined two types of large databases. The first contains information on long-term changes in the frequency of occurrence of flowering plant species (Angiospermophyta), and is based on repeated floristic inventories of over 200,000 grid cells in three countries (the Netherlands, Great Britain, and Germany) recorded over the 20th century. The second is a recently completed database containing quantitative information for more than 20 key plant characteristics for over 3000 vascular plant species in NW Europe. This combination allowed us to compare characteristics of declining and non-declining species. We selected the plant characteristics best able to discriminate between two competing explanations for plant diversity losses (see Table 8.1):

Table 8.1: Variables used in the multiple logistic regressions.
For further details on the classification of dispersal traits see Table 8.2.

Plant characteristic	Classification
Frequency in historical species pool	Number of occupied grid cells in the first recording period (log-3 transformed for the Netherlands, log-2 transformed for Great Britain: 1 (very rare) - 9 (very common))
Dispersal potential water	Potential for Long Distance Dispersal by water (0 = low, 1=high)
Dispersal potential wind	Potential for Long Distance Dispersal by wind (0 = low, 1=high)
Dispersal potential fur	Potential for Long Distance Dispersal by fur of mammals (0 = low, 1=high)
Dispersal potential dung	Potential for Long Distance Dispersal by dung of mammals (0 = low, 1=high)
Dispersal potential birds	Potential for Long Distance Dispersal by bird-droppings (0 = low, 1=high)
No LDD	Species with no attributes for Long Distance Dispersal by any of the 5 vectors considered (0 = no, 1 = yes)
Seed longevity	Persistence in the soil seed bank (0 = seeds persist in the soil < 1 year, 1 = seeds persist in the soil ≥ 1 year)
Nitrogen requirements	Ellenberg indicator value for nitrogen requirements (1 = low, 9 = high)

1) *Nitrogen requirement*. Loss of low-productivity habitats and eutrophication of remaining habitat patches (with associated niche-based processes) are currently regarded as one of the major drivers of species losses in large parts of the world (Vitousek et al. 1997; Bobbink et al. 1998; Grime 2001; Tilman et al. 2002; Stevens et al. 2004).

2) *Dispersal capacity*. The ability to track the changes in habitat configuration, through seed dispersal in space (long-distance dispersal) and / or time (formation of a persistent soil seed bank) can be a major determinant of regional species dynamics (Tilman 1997; Turnbull et al. 2000; Leibold et al. 2004; Ozinga et al. 2005; Nathan 2006). The characteristics considered were seed bank longevity and the capacity for dispersal by the following vectors, all capable of providing effective long-distance dispersal (>100 meters): water, wind, large mammals (both externally through attachment to fur and internally through survival in the digestive tract) and birds (internally).

The relative importance of the two alternative explanations was quantified by means of multiple logistic regression, with decline during the 20th century as the dependent variable and frequency in the historical species pool, nitrogen requirements and dispersal traits of species as independent variables.

Trends in frequency of occurrence during the 20th century

Trends in frequency of occurrence were assessed using published national surveys of the occurrence of vascular plant species in grid cells (quadrats). Since trend data are sensitive to various sources of bias and to differences in spatial and temporal scale (Telfer et al. 2002; Hartley & Kunin 2003; Cheffings et al. 2005; Tamis 2005), we used a binary classification for species trend: declining versus not declining. Stochastic effects of rarity were included in the analysis by assigning to each species a rarity index related to its frequency of occurrence at the beginning of the period over which the trend analysis was performed. Rarity in itself may increase the risk of local extinction due to random processes such as demographic and environmental stochasticity or genetic drift (Gilpin & Soulé 1986; Nee & May 1997; Hubbell 2001; Tilman 2004). The species lists from various data sources were aggregated into one species list using the SynBioSys species checklist (Schaminée et al. 2007; <http://www.synbiosys.alterra.nl/eu/>). Technical details of the survey methods of national lists of declining species differ between countries and therefore the three countries were analyzed separately.

THE NETHERLANDS

Trends during the 20th century were based on the occurrences of plant species in the Netherlands in 1 km² grid cells during two periods: 1902–1949 and 1975–1998 (over 7 million records; Van der Meijden et al. 2000). The analysis was based on a selection of 7,374 grid cells with multiple observations within the grid

cell across both periods (nearly 25% of the land surface of the Netherlands) and corrected for temporal differences in sampling intensity (Van der Meijden et al. 2000; Tamis & Van 't Zelfde 2003; Tamis 2005). Species were labeled as declining if the number of grid cell occurrences had declined by at least 25% over the 20th century, representing local extinction at the 1 km² scale. The historical frequency of occurrence was defined as the log-3 transformed number of grid cells occupied in the 1902–1949 period, ranging from 1 (very rare) to 9 (very common) (Tamis & Van 't Zelfde 2003).

GREAT BRITAIN

The list of declining species for Great Britain was based on the change index published in New Atlas of the British and Irish flora (Preston et al. 2002). The change index is based on the comparison of the results of two nationwide surveys of British plant distribution at a 10 × 10 km scale (1930–1969 and 1987–1999) and takes into account differences in recording intensity (Telfer et al. 2002). In contrast to the change index for Netherlands, this index cannot be interpreted as a percentage of change in the number of occupied grid cells, but refers to the change in the frequency of occurrence compared to that of an 'average species'. The change indices of all species sum to zero. In the present study, species were regarded as declining if they had a change index of -0.30 or less. The historical frequency in the species pool was derived from the log-2 transformed number of 10 × 10 km quadrats for the 1930–1969 period, ranging from 1 (very rare) to 9 (very common).

GERMANY

The list of declining species for Germany is based on the trend index (tendency to decline or increase) given by Ellenberg (2001), ranging from 1 (almost disappeared) to 9 (strongly expanding). This trend index is based on a combination of floristic data over the 20th century and expert judgments by several experienced botanists, and refers to changes in species frequency in 110 km² quadrats and their dominance within these quadrats. The list of declining species includes species that had a trend index ≤ 3. As floristic inventories in the first half of the 20th century in Germany focused on rare species only, it was not possible to find reliable information on species frequency in the historical species pool for all species. Therefore we have analysed the German data without this variable (unlike the two other datasets).

Classification of nitrogen requirement

To compare the effects of changes in the frequency of occurrence due to dispersal limitation with those due to habitat change (e.g. eutrophication), we used Ellenberg indicator values for nitrogen requirement (Ellenberg et al. 2001). These indicator values are species-specific scores, ranging from 1–9, for the optimal occurrence of species along environmental gradients. For Great Britain, we used adjusted

indicator values (Hill et al. 1999). Evidence for the accuracy of Ellenberg indicator values has been provided by several studies reporting a close correlation between average indicator values and corresponding measurements of environmental variables (see Diekmann 2003 for a review). For other habitat factors see Appendix.

Classification of dispersal traits

Data on dispersal ability by various vectors were extracted from the LEDA database (life-history traits of the Northwest European flora; Knevel et al. 2003; 2005) and adapted to a binary classification (see Table 8.2 and Chapter 2). We considered the following dispersal vectors, all capable of providing highly effective long-distance dispersal: water, wind, the fur of large mammals, the digestive tract of large mammals and the digestive tract of frugivorous birds. Humans as complex dispersal vector were not taken into account, as this would involve various trait syndromes, and comparative data for large sets of species are lacking. We aggregated the available data into a binary classification, assigning each species to one of two classes for each dispersal vector: '1' if the species has attributes for long-distance dispersal by a given vector and '0' if the species has no such attributes (see Table 8.2). Although the binary classification of the continuum is less precise for individual species, it allows generalizations at the level of large species pools. It is important to note that many species have a high dispersal potential (i.e. a '1' in the database) for more than one long-distance dispersal vector. As regards dispersal through time, species were classified as being capable of accumu-

Table 8.2: Classification criteria for the capacity for long-distance dispersal by individual dispersal vectors (see Chapter 2 for more details).

Dispersal vector	Criterion
Dispersal potential – water	Propagules float on water surface for at least 7 days
Dispersal potential – wind	Falling velocity of propagules after a phase of acceleration (terminal velocity in m/s): < 0.5 (release height 0.2 m); < 0.6 (release height 1 m); < 0.75 (release height 2 m)
Dispersal potential – dung	High survival of seeds after passing through the digestive tract (at least 3 germinating seeds and relative abundance in dung higher than 5% of relative abundance in the diet) and seeds frequently eaten
Dispersal potential – fur	Propagules with awns, spiny teeth, burrs, pappus with barbs, style with barbs, hooked hairs or excreting viscid substances
Dispersal potential – birds	High survival of seeds after passing through the digestive tract (at least 3 germinating seeds and relative abundance in dung higher than 5% of relative abundance in the diet) and morphological adaptations to attract birds (fleshy fruit)

lating a persistent seed bank if their seeds can remain viable in the soil for ≥ 1 year, as indicated by a seed longevity index ≥ 0.3 (Knevel et al. 2005).

Analysis

The relative importance of nitrogen requirements and dispersal traits for the probability of a negative trend in frequency of occurrence was quantified for each country by means of multiple logistic regression, which is considered an effective method to analyze binary ecological data (McCullagh & Nelder 1989; Austin et al. 1990; Trexler & Travis 1993). The statistical analyses were performed using SPSS 12 (© SPSS Inc. 1989-2003). Variables were entered in the regression model by stepwise forward selection. The parameters of the model were tested for inclusion in the model using the likelihood ratio test, which assesses the improvement of the fit between the predicted and observed values of the response variable caused by adding the predictor variable. Only variables for which the likelihood ratio χ^2 had a P value <0.05 were included in the model. The relative effect of individual variables was assessed by means of Wald χ^2 . Wald statistics and the corresponding probability are based on the squared ratio of the unstandardized logit coefficient to its standard error.

Excluded from the analyses were species restricted to aquatic or alpine habitats, species that are often planted (such as many trees), apomictic species and species groups presenting taxonomic problems (see Van der Meijden et al. 2000 and Preston et al. 2002 for details for the Netherlands and Great Britain, respectively). Actual species numbers are listed in Table 8.3.

Since model parameters for individual variables are expressed as differences in logistic values, which are difficult to interpret in an ecologically meaningful way, the effects of dispersal traits have been illustrated graphically for the Netherlands, the country for which the most detailed information was available.

The robustness of the results was tested for the Dutch dataset, since this dataset has been recorded with the highest resolution and has the smallest proportion of missing values (see Table 8.3). We checked for possible confounding effects due to multicollinearity among variables, pseudocorrelation with other habitat factors and phylogenetic non-independence of species as data points (see appendix).

Table 8.3: Number of species included in the analysis for the three countries (C, total number of species 1274), relative to the total number of terrestrial, non-alpine species (A).

	Netherlands	Great Britain	Germany
A: Total number of terrestrial, non-alpine species	1351	1583	2226
B: Subset of A with trend data	1268 (94%)	1252 (79%)	1851 (83%)
C: Subset of B with data on plant characteristics	1017 (80%)	841 (67%)	1085 (59%)
D: Subset of C labelled as declining	322 (32%)	355 (42%)	558 (51%)

Results

Overall, dispersal traits make a large and significant contribution to explaining interspecific patterns of species losses, of the same order of magnitude as the effect of eutrophication (Table 8.4 and appendix). Interspecific differences in dispersal traits are thus good predictors of the extinction risk for plant species. Despite methodological differences the results are consistent across all three countries (Table 8.4). Moreover, the results proved to be unbiased by possible confounding effects such as multicollinearity among variables, pseudocorrelation with other habitat factors and phylogenetic non-independence of species as data points (see appendix).

The direction of the relationship between dispersal traits and extinction risk differs between dispersal vectors. For each dispersal vector, figure 8.1 shows the percentage of declining species for two subsets of species: with and without a persistent seed bank. Species with a high potential for dispersal in the fur of large mammals or by running water are significantly more likely to decline than those using other dispersal vectors (Figure 8.1). On the other hand, species with a high potential for dispersal by wind or birds are less likely to decline. This is what we had expected, since free roaming furred mammals and freely running water almost disappeared from the Northwest European landscape (see Box 3 for an historical overview). The results also demonstrate that species with the ability to accumulate a persistent soil seed bank ('dispersal through time') perform relatively well.

Independent from the effect of dispersal vectors is the effect of eutrophication. Species that are adapted to nutrient-poor conditions are over-represented among

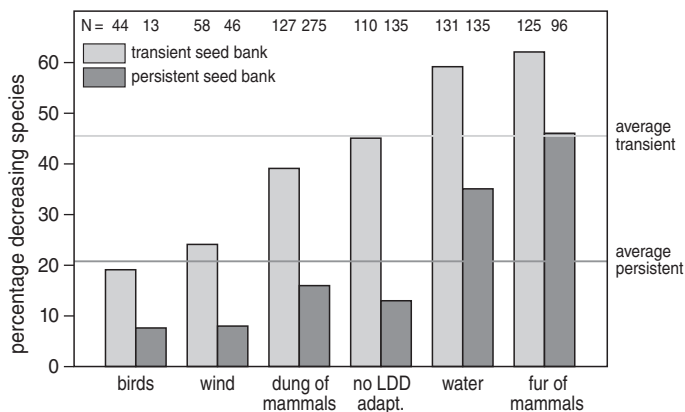


Figure 8.1: Percentage of plant species declining by more than 25% over the 20th century, for five long-distance dispersal (LDD) vectors. Species are divided into two groups for each dispersal vector, according to their ability to accumulate a persistent soil seed bank. Horizontal lines indicate the average percentages (geometric means) for species with a persistent soil seed bank (black) and those with a transient soil seed bank (grey) (data from the Netherlands, the country with the most detailed information on species decline).

Table 8.4: Effects of plant characteristics on the probability of decline. Results are given of Stepwise Multiple Logistic Regressions for three countries, with decline during the 20th century as the dependent variable and plant characteristics as the independent variables. Wald χ^2 gives an indication of the strength of the effect for individual variables. Positive values of B indicate that the decline is increased by the given variable, negative values indicate less than average decline. Model performance as indicated by Nagelkerke's R^2 : Netherlands: 0.40; Germany: 0.20; Great Britain: 0.16. The highest performance in the Netherlands probably reflects the more detailed information on species trends available for that country.

Variable	The Netherlands				Great Britain				Germany			
	B	S.E.	Wald χ^2	Sign.	B	S.E.	Wald χ^2	Sign.	B	S.E.	Wald χ^2	Sign.
Frequency in historical species pool	-0.28	0.04	57.5	<0.001	0.42	0.06	46.3	<0.001	-	-	-	-
Nitrogen requirements	-0.36	0.04	75.6	<0.001	-0.19	0.04	22.1	<0.001	-0.33	0.03	108.1	<0.001
Dispersal potential – fur	1.34	0.19	47.8	<0.001	0.65	0.18	13.5	<0.001	0.83	0.16	25.6	<0.001
Dispersal potential – water	1.21	0.18	46.6	<0.001				n.s.	0.65	0.15	18.8	<0.001
Seed longevity	-1.01	0.17	36.2	<0.001				n.s.				n.s.
Dispersal potential – birds	-1.33	0.42	10.0	0.002				n.s.	-0.91	0.31	8.8	0.003
Dispersal potential – wind	-0.99	0.32	9.7	0.002	-0.83	0.29	8.3	0.004	-0.46	0.23	4.0	0.047
Dispersal potential – dung				n.s.	-0.33	0.15	4.5	0.035				n.s.
No LDD				n.s.				n.s.				n.s.
Constant	2.36	0.30	64.0	<0.001	-2.24	0.46	24.208	<0.001	1.29	0.17	60.1	<0.001

the declining species. Interspecific differences in the risk of a negative population trend can thus be predicted from the interplay of nitrogen requirements (indicating risks on local extinction due to eutrophication) and adaptations to various dispersal vectors. On the other hand, there is no consistent effect of historical abundance. We expected rare species to be more likely to decline (cf. Pimm et al. 1988, Hubbell 2001). This is true for the Netherlands, but the opposite is true in the UK.

Discussion

Our results imply that differences between species in adaptations to various dispersal vectors are an important but largely overlooked factor in explaining losses in plant diversity in Northwest Europe in the 20th century, with water- or fur-assisted dispersal being over-represented among declining species. Our analysis indicates that dispersal limitation due to a degraded dispersal infrastructure is no less important in explaining declines in regional plant diversity than the effects of eutrophication and associated niche-based processes.

Several authors have suggested that many species show a delayed response to habitat fragmentation and degradation due to time lags in local extinction (the so called 'extinction debt', Tilman et al. 1994; Eriksson 1996; Stöcklin & Fischer 1999). There may be also a delay, following degradation of the services provided by dispersal vectors, before species reach a new equilibrium corresponding to the dispersal services currently provided by the landscape. Present-day distribution patterns of many species that are highly dependent on dispersal by water or the fur of large mammals may therefore reflect vanished landscape configurations with a more diverse dispersal infrastructure. These spatial distribution patterns may be regarded as reflecting the 'ghost of land-use past' (cf. Harding et al. 1998). This 'ghost' thus represents present-day ecological effects of past changes in the dispersal infrastructure, and may also be important in predicting the degree to which plant species can track changes in the landscape e.g. due to ecological restoration or climate changes (cf. Thomas et al. 2004).

Traditional habitat restoration measures that are directed at improving local habitat quality, although very useful, may therefore be not sufficient to halt losses in plant diversity. Our findings clearly show that survival of sessile plant species in fragmented landscapes requires 'moving corridors' such as free flowing waters, dispersing birds and free ranging or herded large mammals. Hence, the effects on the regional persistence of endangered vascular plant species provided by ecological networks such as the EU's prestigious and costly 'Nature 2000' framework will depend critically on the parallel conservation or restoration of an appropriate infrastructure of dispersal vectors. Otherwise conscientious but deliberate re-introduction schemes need to be discussed.

Appendix – Check for possible confounding effects

The robustness of the results was tested for the Dutch dataset, since this dataset has been recorded with the highest resolution and has the smallest proportion of missing values (see Table 8.3) and changes in frequency of occurrence are more marked at more detailed spatial scales (Thomas & Abery 1995, Kunin 1998, Witte & Torfs 2003, Tamis 2005).

Correlations between variables

A potential problem in evaluating the importance of individual variables is that they might be interrelated (multicollinearity). We checked for this potential confounding effect in two ways.

Firstly, we calculated Pearson correlations between the explanatory variables. Plant characteristics were only weakly correlated between species ($r < 0.25$ for all combinations, with the highest correlations between ‘Dispersal potential – dung’ * ‘Seed longevity’: $r = 0.23$ and ‘Nitrogen requirements’ * ‘Seed longevity’: $r = 0.22$).

Secondly, we used a combination of conditional and marginal tests (e.g. McCullagh & Nelder 1989). In conditional testing, the variable is added to the simplest regression model (only including the constant) whereas in marginal testing, the variable is entered in the full model (the constant and all other significant variables except the variable of interest). If the contributions of the variables of interest are similar in both tests, this implies a reliable estimate of the relative importance of the given variable. Table A8.1 indicates that multicollinearity was not a problem. Interaction effects were tested but these did not change the effect of the dispersal vectors on the risk of species decline.

The difference in response between species with a high capacity for dispersal by the dung of large mammals and those dispersed by their fur seems surprising at first glance. This finding can be understood from the fact that species dispersed in dung are generally less specialized in terms of dispersal attributes than those with specialised attributes for dispersal in fur (Janzen 1984, Pakeman et al. 2002, Cuvreur et al. 2005), and are thus less dependent on the availability of large herbivores than species with fur-assisted seed dispersal.

Pseudocorrelation with other environmental factors

Dispersal services for propagules may be correlated with living conditions for established plants in their environment. In particular, dispersal services by water may correlate with the moisture environment of the established plants, while dispersal services by large mammals may correlate with the light conditions in open, grazer-dominated vegetation (Ozinga et al. 2004). To evaluate the role of the environment of the established plants (in terms of moisture, light and nitrogen), as compared to that of the dispersal services, we calculated two models: an ‘environmental model’ (excluding dispersal characteristics), and a ‘dispersal

Table A8.1: Results of marginal and conditional testing of individual variables and performance of variables in the ‘environmental model’ and the ‘dispersal model’.

Plant characteristic	Marginal testing			Conditional testing		Environmental model		Dispersal model	
	Wald χ^2	Sign.	R ²	Wald χ^2	Sign.	Wald χ^2	Sign.	Wald χ^2	Sign.
Frequency in historical species pool	67.4	<0.001	0.095	56.2	<0.001	60.6	<0.001	70.9	<0.001
Nitrogen requirement	100.7	<0.001	0.150	68.6	<0.001	95.1	<0.001		
Moisture		n.s.		6.4	0.011	16.1	<0.001		
Light requirements	12.4	<0.001	0.018		n.s.		n.s.		
Dispersal potential									
–water	– 39.5	<0.001	0.053	30.1	<0.001			42.1	<0.001
–wind	11.1	0.001	0.018	7.5	0.006			6.5	0.011
–fur	67.0	<0.001	0.090	47.8	<0.001			40.7	<0.001
–dung	21.8	0.006	0.031		n.s.			n.s.	<0.001
–birds	7.6	<0.001	0.013	6.9	0.009			9.6	0.002
No LDD		n.s.			n.s.				n.s.
Seed longevity	64.1	<0.001	0.089	27.7	<0.001			55.1	<0.001

model’ (excluding the environmental variables; see Table A8.1). Moisture and light requirements of plant species were obtained from the corresponding Ellenberg indicator values, as explained in the main document for nitrogen (Ellenberg et al. 2001, see review by Diekmann 2003 on the accuracy of these indicator values). We found that the dispersal model performed better than the environmental model (Nagelkerke’s $R^2 = 0.32$ and 0.23 , respectively; Table A8.1). This means that relationships between species trends and dispersal services cannot be explained as pseudocorrelations driven by an underlying correlation between trends and the environment of the established plants.

Phylogenetic non-independence

The observed patterns might be partly phylogenetically induced if related species have similar characteristics and extinction risks due to their common ancestry (phylogenetic conservatism, e.g. Harvey & Pagel 1991). In order to check for possible confounding effects of such phylogenetic non-independence, we performed a post-hoc test of bivariate relationships between each of the independent variables and the species trend, using phylogenetically independent contrasts (Harvey & Pagel 1991). Phylogenetically independent contrasts are comparisons between sister taxa, each comparison describing the outcome of a separate, i.e. independent, evolutionary divergence of lineages. The contrasts were calculated exclusively

Table A8.2: Test results for bivariate comparisons across phylogenetically independent contrasts. The numbers of contrasts with non-zero differences between the species were compared. The table shows the percentage of cases in which these differences were positive (i.e. where the declining species had a higher value than the non-declining species), and the corresponding Z and P values (two-tailed). Note that only dispersal potential for fur and dispersal potential for water were overrepresented among declining species.

	N contrasts	Percentage	Z-value	Sign.
Frequency in historical species pool	200	27.5	6.29	<0.0001
Nitrogen requirements	195	28.7	5.87	<0.0001
Dispersal potential – fur	65	78.5	4.47	<0.0001
Dispersal potential – water	89	73.0	4.24	<0.0001
Seed longevity	121	24.8	5.50	<0.0001
Dispersal potential – birds	11	36.4	0.60	0.5565
Dispersal potential – wind	33	9.1	4.53	<0.0001
Dispersal potential – dung	65	32.3	2.73	0.0064
No LDD	68	32.4	2.79	0.0053

between extant species, using the ‘Brunch’ routine of the CAIC computer program (Purvis & Rambaut 1995; following Burt 1989). This method does not make any assumptions about the mode of trait evolution and does not try to reconstruct ancestral states, making it suitable for dichotomous variables and permitting analysis by sign tests (Purvis & Rambaut 1995, Prinzing et al. 2002). The results (Table A8.2) largely confirmed our above analysis across species as independent data points. For all variables except dispersal capacity by birds, the relationship with the risk of decline was significant and in the same direction as in the across-species analysis.

Box 3: Overview of changes in dispersal infrastructure in the Netherlands

Several vectors have a high potential for the transport of seeds between sites, including water, wind, birds and large mammals, each with their own characteristics (Fischer et al. 1996, Poschlod & Bonn 1998, Boedeltje et al. 2003, Manzano & Malo 2006, Nathan 2006). At the landscape level, these dispersal vectors act like a complex 'dispersal infrastructure'. In Northwest Europe, wind patterns and bird migrations remained almost unchanged throughout the 19th and 20th centuries (KNMI 2005 respectively LWVT / SOVON 2002), while the exchange of large mammals and water between sites has greatly decreased. These changes mostly took place some 50 to 150 years ago (Ridley 1930, Beaufoy et al. 1994, Dynesius & Nilsson 1994, Poschlod & Bonn 1998, European Environment Agency 2003, Poschlod et al. 2005). This section presents an overview of the major changes in dispersal infrastructure in the Netherlands.

Free-ranging or herded large mammals

During the end of the Pleistocene and the beginning of the Holocene, most large mammalian species and all 'megaherbivores' became extinct in the Netherlands as well as in other parts of Northwest Europe (Anderson 1984, Stuart 1991, 2005). Since there is a positive log-linear relation between body weight and dispersal distances (as regards both median and maximum dispersal distances, Sutherland et al. 2000), the most effective long-distance dispersal vectors among the mammals have thereby probably disappeared. Only four widely distributed ungulate species have remained in the Netherlands (in order of increasing median dispersal distances): Roe deer (*Capreolus capreolus*), Fallow deer (*Dama dama*), Wild boar (*Sus scrofa*) and Red deer (*Cervus elaphus*). The natural migration of these remaining wild mammalian species is currently severely hampered in most European landscapes (Wallis de Vries 1995, Groot Bruinderink et al. 2003).

Grazing by livestock, i.e. horses, cattle, sheep, goats and pigs, can be regarded as a modern analogy of seed dispersal by the original fauna (Janzen & Martin 1982). Until the beginning of the 20th century, it was common for farmers to herd their livestock on a daily basis on the unfenced pastures, covering distances of approximately 0.5 to 10 km (see Figure Box 3.2). The highly branched networks of drift-roads for livestock around the villages remained in use for many centuries (Edelman 1934, Slichter Van Bath 1980, Jager 1985, Bielemans 1987, Hillegers 1993, Renes 1997, Elerie 1998, Spek 2004).

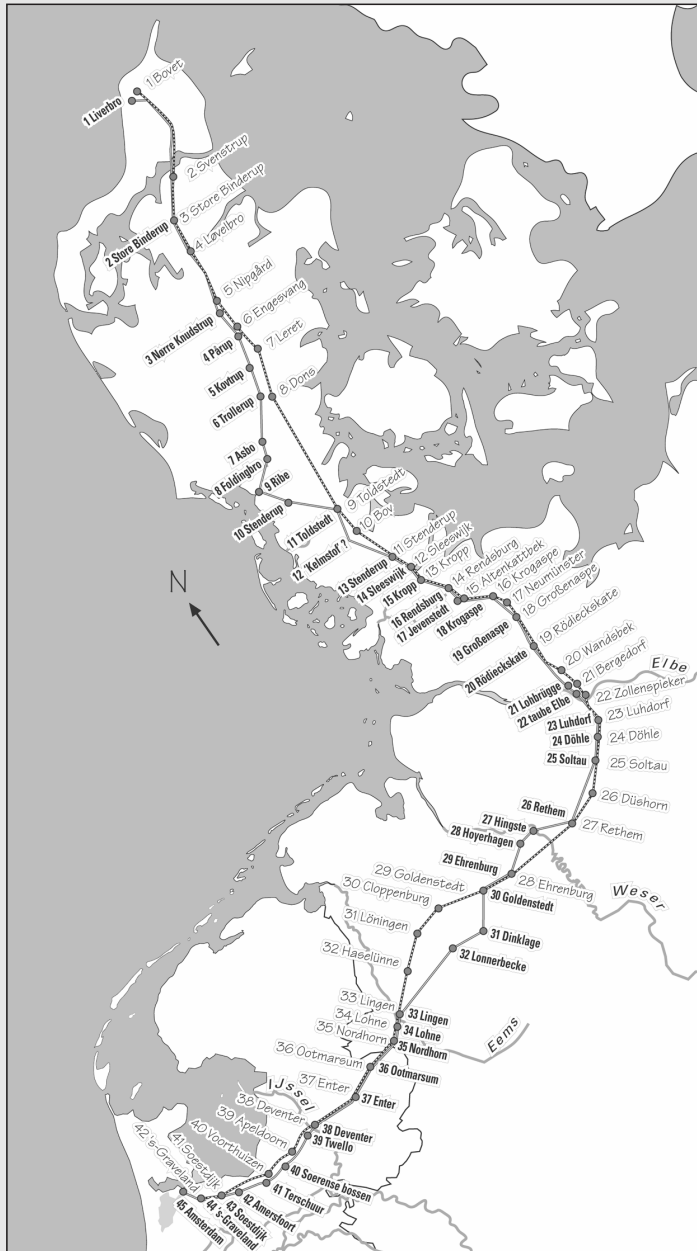


Figure Box 3.1: Example of inter-regional dispersal infrastructure: Inter-regional ox route between stalls in the north of Jutland (Denmark) to meadows in the province of Holland as described in two documents from 1731 (based on Gijsbers 2002 with some modifications). This route was used on a yearly basis from the 15th century until the 18th century and the transport took about six weeks.



Figure Box 3.2: Example of local dispersal infrastructure in the Northern part of the Netherlands as deduced from an old military map of Hottinger (1792-1794). The map shows in the middle part a dry sandy ridge with the main regional livestock drift route between Groningen and Coevorden (1). Archeological evidence revealed that this route was used for more than thousand years. The lower and upper part of the map show the river valley of the Drentsche Aa (2: main course) and the Hunze (3). Both river valleys were to a large extent used as ‘common grounds’ (owned by the community) for the grazing of cattle and the areas were interconnected by a fine-meshed network of local livestock drift roads. This network of drifts was used for many centuries, e.g. in the south-western part the road from the Wolddeelen towards ‘t Hemmerik (4) and in the north-eastern part the road bordering De Koelanden (5). Along the livestock drifts species-rich fringe communities occurred and some small remnants persisted into present time with relic populations of plant species from ancient landscapes like *Gagea lutea*, *Leonurus cardiaca*, *Marrubium vulgare* and *Viola riviniana*. The lower parts near the river were almost yearly inundated, including artificial winter-inundations till 1913. The grasslands in these areas were used as hay-meadows (e.g. Glimmer hooyland), and in drier years for grazing at the end of the season. Thanks to several old vegetation descriptions (e.g. by De Leeuw, Vlieger & Westhoff in 1937 in ‘t Hemmerik) an impression can be gained of the species rich grassland communities with *Calamagrostis stricta*, *Carex appropinquata*, *C. diandra*, *C. hostiana*, *Cirsium dissectum*, *Dactylorhiza incarnata*, *Fritillaria meleagris* and *Serratula tinctoria*.



Figure Box 3.3: Herded sheep flock in the Drentsche Aa valley near Glimmen. In the Netherlands this traditional way of livestock transport along drift roads has nearly disappeared. The photo shows a drift road that is still used on a yearly basis (see 4 in Figure Box 3.2). Herded livestock movements provide the opportunity for directed seed dispersal.

From the 15th century onwards, it became common in the Netherlands to transport livestock between regions (over distances of 20–200 km) for trade (Wiese 1966, Bieleman 1987, Hillegers 1993, Gijsbers 1999, 2002). These migratory livestock systems (transhumance) existed in large parts of Europe (Ruiz & Ruiz 1986, Whittaker 1988, Tack et al. 1993, Frizell 1996, Poschlod & Bonn 1998, Bruun & Fritbøger 2002). Although the seasonal transhumance was potentially important for the migration of plant species over very long distances (>100 km; Fischer et al. 1996, Poschlod & Bonn 1998, Manzano & Malo 2006), the herded livestock within regions was probably much more important for seed dispersal in a quantitative sense. Interregional drift of livestock was restricted to a few main drove-roads (see Figure Box 3.1 and 3.2). By contrast, the daily, local herding of livestock encompassed much larger areas with a higher frequency (Jager 1985, Gijsbers 1999, Spek 2004; Figure Box 3.2).

Nowadays, free-ranging or herded livestock grazing has become rare in Northwest-Europe (Figure Box 3.3. Its spatial coverage has been reduced by more than 90% in the Netherlands (Slichter Van Bath 1980, Bielemans 1987, Spek 2004) and by 75% in many other parts of Northwest Europe (Beaufoy et al. 1994, Bignal & McCracken 1996, Poschlod & Bonn 1998, Bruun & Fritbøger 2002, Bunce et al. 2004). Free-ranging or herded livestock grazing has been replaced by grazing in fenced fields or livestock housing. This in turn has greatly reduced the potential for mammal-assisted dispersal of plants between sites (Fischer et al. 1996, Poschlod & Bonn 1998, Manzano & Malo 2006).

Free-running and inundating water

Palaeo-ecological evidence shows that prior to the human inference, the hydrology of many European lowland rivers was dynamic, with multi-braided channels influencing large stretches of land (Brown 2002). In many floodplains in Northwest Europe, inundations were tolerated, and from the Late Middle Ages onwards even stimulated due to the positive effects on grassland productivity (Klapp 1971, Rackham 1986, Ellenberg 1988, Thissen & Meijer 1991, Pott 1995, Konold 1997, Bonn & Poschlod 1998, Elerie 1998, Burny 1999, Baaijens et al. 2001, Evard 2005). In rivers throughout Europe, however, natural flood regimes have been altered severely by large flow- and flood-control projects implemented during the 19th and 20th century (Dynesius & Nilsson 1994, Lytle & Poff 2004, Nilsson et al. 2005). As a result, the area affected by frequent inundations has been greatly decreased over the last two centuries, in the Netherlands (Gottschalk 1977; Kalweit 1993) as well as in many other parts of Europe (Dynesius & Nilsson 1994, Brown 2002, Lytle & Poff 2004, Nilsson et al. 2005). It is estimated that more than 90% of European floodplains are now cultivated and therefore functionally 'extinct' (Tockner & Stanford, 2002). For example, it has been estimated that until 1860, up to 60% of the total area of the province of Overijssel was inundated periodically with surface water or groundwater during the winter period, while this area is now reduced to less than 1% (Corporaal et al. 2002). The restriction of transversal and longitudinal water flows has therefore greatly reduced the potential of seed dispersal between sites (Dynesius & Nilsson 1994, Poschlod & Bonn 1998, Jansson et al. 2000, Lytle & Poff 2004, Boedeltje et al. 2003).



Synthesis: The role of dispersal in the assembly of plant communities

Wim A. Ozinga

Biodiversity crisis challenges the search for assembly rules

Growing concern about the ongoing loss of biodiversity has resulted in increased efforts throughout the world to protect endangered species and to conserve and restore endangered ecosystems (Schemske et al. 1994, United Nations 2002, Delbaere 2002, Balmford et al. 2005). In view of the large input of financial and human resources into nature conservation and restoration, increasing our insights into the mechanisms that threaten species and ecosystems is therefore one of the great scientific challenges of the 21st century. This is of particular importance for plant species, not only because they are the primary producers upon which a whole suite of species higher up in the food chain depend, but also because plants, due to their sessile nature, are particularly vulnerable to changes in their habitat beyond the variation they are adapted to.

Nature conservation and restoration as currently practised has been criticized by several authors for not being founded on a solid conceptual basis (Schemske et al. 1994, Hobbs & Norton 1996, Simberloff 2004, Temperton et al. 2004, Hodgson et al. 2005, Van Andel & Aronson 2005). More generally, the field of ecology has been criticized for its lack of general rules (Lawton 1999). This criticism should be taken seriously, since current conservation and restoration efforts regularly fail to produce the results expected at the start of restoration projects. When such large-scale tests of ecological paradigms fail, they represent a challenge to rethink the underlying general principles. The rules that determine the assembly of local plant communities from the pool of regionally available species (so-called '*assembly rules*', Diamond 1975) can be regarded as such a general principle. These assembly rules govern the success of efforts to conserve and restore plant diversity, the basic prerequisite for the conservation and restoration of nature.

Three sets of assembly processes

There is now a wealth of theories on the processes that shape the species composition of local plant communities, theories that can be grouped into three broad views according to the main processes involved (Chapter 1):

Niche assembly

The niche-based view of community assembly asserts that local species composition (within habitat patches) is a deterministic consequence of local interactions between the extant species in a plant community and their environment, based on differences between species in terms of resource usage, stress tolerance and disturbance resistance, which determine these interactions (e.g. Hutchinson 1961, Grime 1977, 2001, Tilman 1985, Ellenberg 1988, Berendse et al. 1992, Keddy

1992, Chase & Leibold 2003, Silvertown 2004). Spatial and temporal heterogeneity of local environmental conditions (both abiotic and biotic) then results in niche segregation between species and in the sorting of species along environmental gradients within and across habitat patches. The limited availability of microsites with specific environmental conditions for germination and subsequent survival has been called ‘microsite limitation’ (Eriksson & Ehrlén 1992, Zobel et al. 2000, Munzbergova & Herben 2005).

Dispersal assembly

The dispersal-based view of community assembly focuses on larger spatial and temporal scales and assigns a more prominent role to differences between plant species in their ability to track regional dynamics of habitat patches through long-distance seed dispersal and/or through dispersal in time by means of a persistent soil seed bank. In this view, plant species regularly go locally extinct by chance, which is compensated by new colonizations. Plant properties (traits) that affect dispersal ability in space or time influence the rates of colonization and extinction of habitat patches (e.g. Grime & Hillier 1992, Tilman 1997, Turnbull et al. 2000, Foster et al. 2004, Fenner & Thompson 2005, Ozinga et al. 2005b). Local communities occupying habitat patches are then embedded in so-called ‘metacommunities’ and are connected to each other by dispersal (Mouquet & Loreau 2002, Leibold et al. 2004).

Trait-neutral assembly

The trait-neutral view of community assembly (Hubbell 2001, Bell 2001) also assigns a prominent role to the availability of seeds, but in contrast to the dispersal assembly view, the trait-neutral view suggests that plant traits are not important in determining species abundance patterns in terms of their frequency of occurrence. In the trait-neutral view, community assembly can be understood solely from species-specific differences in regional abundance, which strongly affect the extinction and colonization probabilities. Thus, species are common or rare purely by chance. Although this view is in strong contrast to the other two, more common views, it performs surprisingly well in describing patterns of relative abundance of species within and across communities, at least in tropical forests (Hubbell 2001, Volkov et al. 2003, 2005).

The three sets of driving processes thus correspond to different limiting factors for community assembly (see Table 9.1). The three views of community assembly can be tested using a two-step procedure. The first step involves assessing the relative importance of ‘microsite limitation’ versus ‘seed limitation’ in the assembly of plant communities. If seed limitation is indeed an important factor explaining local plant biodiversity, the subsequent second step is to assess the relative importance of trait-neutral ‘seed-source limitation’ versus trait-based ‘dispersal limitation’.

Table 9.1: Simplified overview of driving processes and limiting factors in the three main views of the assembly of plant communities.

View of community assembly	Driving process	Limiting factor	
Niche-based view	Sorting of species along environmental gradients (within and across habitat patches) based on differences between species in exploiting these conditions (niche-related traits)	Abundance of microsites with a suitable environment for establishment and subsequent survival (<i>microsite limitation</i>)	
Dispersal-based view	Sorting of species across habitat patches differing in spatial and temporal isolation based on differences between species in terms of dispersal abilities (dispersal traits)	Degree of long-distance seed dispersal (<i>dispersal limitation</i>)	Availability of seeds in habitat patches (<i>seed limitation</i>)
Trait-neutral view	Sorting of species across habitat patches, based on differences between species in their regional abundance, in combination with the overall rate of seed dispersal in the metacommunity (abundance driven; traits do not matter).	Abundance of nearby populations that act as seed sources (<i>seed-source limitation</i>)	

Reconciling microsite limitation and seed limitation

How predictable is local species composition from assembly rules?

PREDICTABILITY FROM ENVIRONMENTAL CONDITIONS

Present-day nature conservation efforts have to a large extent adopted the niche-based view of community assembly. The basic assumption is that local species composition is largely a deterministic consequence of local environmental conditions which filter species from the available species pool according to their niche-related traits. As a consequence, local communities are assumed to be saturated with species, and the absence of a species in this niche-based view indicates that environmental conditions are not suitable. Nature managers therefore focus on influencing local environmental conditions and are funded accordingly (e.g. Bal et al. 2001, European Commission 2003). This poses the question how predictable species composition really is from environmental conditions.

Chapter 3 revealed that species do indeed show a clear sorting along environmental gradients and that species composition across habitat types can be reliably predicted from a few key environmental conditions, such as the availability of (1) water, (2) limiting nutrients (correlated with pH), and (3) light. These environmental variables can therefore be used as predictors ('filters') to compose a list of species that are potentially able to coexist in small-scale habitat patches within a given habitat type (*Habitat Species Pool*). Together, these environmental gradients define a kind of multidimensional 'environmental envelope' or 'habitat templet' (cf. Southwood 1988) in which different positions feature a characteristic combination of species. These filters are particularly effective during the germination and establishment phase (Grubb 1977, Eriksson 2002, Poorter 2007) and together determine the degree of microsite limitation within a habitat patch.

PREDICTABILITY FROM DISPERSAL TRAITS

Despite the clear sorting of species along environmental gradients, Chapter 3 also revealed that at the scale of individual plots (samples from a habitat patch), many species were lacking whose presence might be expected given the combination of environmental conditions. In fact, the predictability of the actual occurrence of individual species in plots was low, with over 90% unexplained variation. According to Chapters 3 and 6, this low predictive power can be explained by seed limitation, which thus seriously reduces the match between species composition and local environmental conditions.

At the species level, the predictability of the occurrence of species from environmental conditions was significantly and positively related to the ability for long-distance dispersal and to adult longevity, and to a smaller extent to the ability to accumulate a persistent soil seed bank (Chapter 3). Species with low dispersal abilities are thus characterized by the frequent phenomenon of suitable, but unoccupied habitat patches. The widespread occurrence of these so-called 'empty habitat patches' (from the species' perspective, cf. Hanski 1998) is in line with the results of many seed addition experiments (Hubbell et al. 1999, Turnbull et al. 2000, Zobel et al. 2000, Foster & Tilman 2003, Xiong et al. 2003, Mouquet et al. 2004).

PREDICTABILITY FROM REGIONAL ABUNDANCE

At the landscape level, it became clear from the comparison between regional and local species composition that the probability of local occurrence is strongly affected by the abundance of species in the regional species pool and not merely by species-specific niche-related or dispersal traits (Chapter 6). This implies that trait-neutral, stochastic dispersal processes also play an important role in community assembly.

Briefly, the results indicate that the availability of seeds greatly increases the degree to which plant species can track suitable habitat patches, and that the degree of seed limitation differs for individual plant species and across landscapes. Both are discussed in more detail in the second part of this chapter ("Two components of seed limitation").

Trade-offs between niche traits and dispersal traits

To reconcile the three views of community assembly it may be fruitful to search for relationships among traits that equip species for local survival and traits that determine their dispersal ability. If trade-offs between functional traits lead to an equalization of variation in fitness across species (i.e. species having the same chance to be present in the next generation) this might in fact be the ultimate reason why the trait-neutral view of community assembly performs so surprisingly well in describing patterns of relative abundance of species within and across communities (cf. Hubbell 2005, 2006). These quasi-similar species (in terms of their fitness) can then co-exist because the time to competitive exclusion is very long (cf. Hubbell & Foster 1986, Hubbell 2006, Scheffer & Nes 2006, Adler et al. 2007). Trade-offs may therefore provide a clue to reconcile trait-based and trait-neutral views of community assembly.

At regional scale, low dispersal abilities can probably be counterbalanced by a higher local aboveground persistence, i.e. greater competitive abilities or greater stress tolerance, leading to lower rates of local aboveground extinction (Tilman 1994, Eriksson 2000, Grime 2001, García & Zamora 2003). Local aboveground persistence and dispersal in space or through time can thus be regarded as alternative regeneration strategies for regional persistence. Chapter 4 indeed presents some empirical evidence for the existence of a ‘persistence – dispersal trade-off’ across a large set of plant species. This relationship, however, is not very strong and probably includes more dimensions. Moreover there are several species that ‘escape’ this trade-off by combine high local persistence with high dispersal abilities (see Chapter 4 for a further discussion). Even though this persistence – dispersal trade-off is far from perfect, if is able to equalize variation in fitness across species to some degree, then niche-based traits and dispersal traits would be less independent than might be expected at first glance.

Two components of seed limitation: seed-source limitation and dispersal limitation

The availability of seeds in a habitat patch (i.e. seed limitation) is based on two components (cf. Clark et al. 1998, Nathan & Muller-Landau 2000; see Table 1).

Firstly, *seed-source limitation* depends on the probability of seeds arriving at a site if seeds are randomly dispersed within the area being studied. This component is thus independent of plant properties (trait-neutral, cf. Hubbell 2001) and the probabilities are solely determined by the abundance of seed sources in a given region.

Secondly, the degree of *dispersal limitation* reflects the degree to which the actual transport of available seeds is reduced (e.g. Clark et al. 1998). This reduction in seed transport might be caused by interspecific differences in long-distance dispersal ability (trait-mediated) or by properties at the ecosystem or landscape level.

Seed-source limitation: the importance of abundance-driven processes

At the landscape level, the results reported in Chapter 6 reveal that the probability of local occurrence is strongly affected by the abundance of seed sources in the regional species pool, rather than merely by species-specific niche-related or dispersal traits. This finding is consistent with predictions from the trait-neutral view of community assembly (Bell 2000, Condit et al. 2000, Hubbell 2001, Tilman 2004, Volkov et al. 2003). This can be explained by increasing rates of colonization of unoccupied habitat patches with increasing densities of seeds across the landscape, leading to a shift in the dynamic balance between colonization and extinction, to the advantage of the former (Levins 1969, Dalling et al. 1998, Hanski 1998). In addition, frequent re-colonizations of microsites in already occupied habitat patches can buffer local communities against local extinctions (the so-called ‘rescue effect’: Brown & Kodric-Brown 1977, Hanski 1983, 1998). In effect, recruitment thus takes the form of a lottery (cf. Chesson & Warner 1981) and the chances in this ‘*recruitment lottery*’ for a given habitat patch are largely dictated by the abundance of species in the regional species pool.

The availability of propagules across landscapes (*‘propagule pressure’*) is probably also an important factor explaining the success of invasive species (Salisbury 1953, Grime 1986, Davis et al. 2005, Lockwood et al. 2005, Von Holle & Simberloff 2005, Hooftman et al. 2006). Rapid increases in propagule pressure may relate to species attributes such as a short time to reproduction, high propagule production and small seeds (Kolar & Lodge 2001, Hamilton et al. 2005), but also to habitat characteristics such as ruderalization, leading to increased availability of unused resources (Davis et al. 2000, 2005, Tilman 2004). Once a species has established a high regional abundance, it can maintain itself merely by dominating the seed rain. At the same time, the pre-emption of many microsites may reduce the chances in the recruitment lottery for other species. Invasive species therefore cause changes in species composition in metacommunities at both local and regional scales. Novel combinations of species that have never occurred before within a given biome may eventually lead to novel ecosystems with new properties, for which the term ‘*emerging ecosystems*’ has been coined (Milton 2003, Hobbs et al. 2006, Vanandel & Aronson 2006).

Dispersal limitation: a key to understanding plant diversity losses

Although the existence of dispersal limitation is well established, the processes that might influence the degree of dispersal limitation are poorly known. Dispersal assembly rules appear to operate simultaneously on at least three levels of organization (species, community and landscape).

SPECIES LEVEL: SLOW VERSUS FAST SPECIES

The importance of dispersal traits in explaining probabilities of local occurrence seems to be overridden by that of the availability of seed sources (Chapter 6, Bell 2000, Condit et al. 2000, Hubbell 2001, Volkov et al. 2003). The importance of

trait-neutral processes, however, does not imply that differences between plant species in terms of dispersal ability do not matter. At the species level, the probability of local occurrence, given the frequency in the regional habitat species pool, is clearly affected by dispersal traits (Chapters 3 and 6), the most important of which is propagule weight. Species with a high propagule weight and low dispersal abilities ('slow species') are underrepresented in local communities and hence leave many suitable habitat patches unoccupied.

Moreover, in many landscapes, human impacts increase the turnover rate of habitat patches (Pickett & Thompson 1978, Dale et al. 1998, Opdam et al. 2003). Slow plant species are apparently less able to keep up with these increased habitat dynamics (Chapters 3 and 8, Bossuyt et al. 1999, Keymer et al. 2000, Matlack 2005, Vellend et al. 2006). As a consequence, in fragmented and dynamic landscapes, immobile plant species may gradually be replaced by invasive species with a more generalist dispersal syndrome.

COMMUNITY LEVEL: INTERACTIONS BETWEEN NICHE ASSEMBLY AND DISPERSAL ASSEMBLY

In our study, dispersal traits showed distinct patterns along the major environmental gradients (Chapter 5). These trait-environment patterns were much stronger at the community level than at the species level, which implies a non-random selection of species from the regional species pool in terms of their dispersal traits. The efficiency of dispersal thus depends on the environmental context.

Species with high dispersal abilities prevail in habitats with large-scale or high-intensity disturbances, while adaptations for long-distance dispersal are less common in late successional stages (Chapter 5). This is empirical proof of the assumption that in communities with a harsh disturbance regime, a selective advantage is gained by those species that succeed in spreading high densities of propagules across large parts of the landscape (Levin et al. 1984, Venable & Brown 1988, Grime 2001).

Moreover, in habitat types with an open vegetation structure, the occurrence of species that are effectively transported by multiple dispersal vectors ('polychory') appears to be the rule rather than the exception (Chapter 5). These differences between communities in the proportion of species that have the potential to 'use' multiple dispersal vectors probably imply that communities differ in their sensitivity to habitat fragmentation. This is shown in Fig. 9.1, where the degree of polychory (ability to be dispersed by multiple dispersal vectors) of species is plotted against vegetation structure, represented by a gradient of light availability. The figure distinguishes between 'core species', which are present in most habitat patches, and 'satellite species', which are usually absent from a given habitat patch. In communities with an open vegetation structure, core species have a higher average colonization capacity, while at the other end of the light availability gradient, there are no significant differences between core and satellite species.

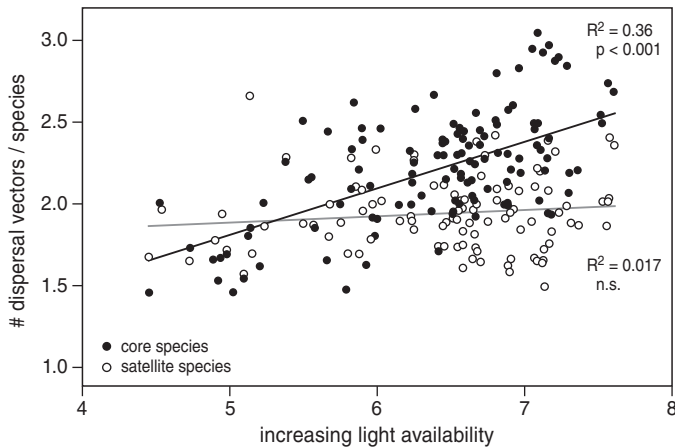


Figure 9.1: Relationship between dispersal ability and frequency of occurrence along a gradient of light availability (based on data from Chapter 5). Dispersal ability is expressed as the mean number of dispersal vectors by which the component species may be efficiently dispersed over long distances. Each dot represents a community type, and the communities have been arranged along a gradient of increasing light availability. Filled and open symbols form paired data: filled symbols represent ‘core species’, which are usually present, while open symbols represent ‘satellite species’, which are usually absent from a given community type.

The absence of a detectable impact of polychory in shaded forest habitats might be caused by the fact that other traits are more important in these habitats, or alternatively that stochastic processes have a higher impact in forests. The latter option would be consistent with the trait-neutral view of community assembly (Hubbell 2001) and with observations of colonization patterns in gaps in tropical forests (Hubbell & Foster 1986, Hubbell et al. 1999, Brokaw & Busing 2000, Volkov et al. 2003, 2005, Condit et al. 2006).

LANDSCAPE LEVEL: THE DISPERSAL INFRASTRUCTURE

The most important finding of our research is the apparent impact of large spatial and temporal scales in explaining losses of plant diversity. Differences in the rates of decline between species do not only depend on inherent differences between species and habitats. The results of our studies clearly demonstrate the importance of past changes in dispersal services at landscape scale for today’s biodiversity crisis (Chapter 8). The crucial process of seed dispersal depends on the availability of dispersal vectors which together act like a complex ‘dispersal infrastructure’. The characteristics of the dispersal infrastructure can vary in space and time, which may induce changes in local species composition (Chapter 8).

Although changes in the relative availability of dispersal vectors during the 20th century have been documented in many parts of the industrialized world (e.g. Ridley 1930, Janzen 1984, 1988, Milton et al. 1990; see review by Poschlod

& Bonn 1998; see Box 3), their impact on plant diversity has never been examined in large-scale studies. Dispersal by water has been restricted by regulation of the natural flood regimes of rivers and brooks for the purpose of flood control, while dispersal by large mammals has declined due to the change from livestock grazing on common grounds to grazing in fenced fields or indoor livestock farming. These changes mostly took place some 50 to 150 years ago and their effects are only now becoming visible.

Differences between species in their adaptations to various dispersal vectors appear to represent a key factor in explaining losses of plant diversity in North-west Europe during the 20th century, with water- or fur-assisted dispersal being over-represented among declining species, while other vectors (wind- or bird-assisted dispersal) are under-represented (Chapter 8). Our results imply, contrary to common belief, that changes in the 'dispersal infrastructure', in combination with changes in the regional abundance of seed sources, are as important in explaining plant diversity losses as the more commonly accepted changes in habitat quality. Our findings call for a thorough rethinking of the spatial and temporal scales of our plant conservation strategies, based on regional species pools and habitat configurations, and on time scales of decades, which together represent the 'ghost of the landscape past'.

Community assembly as an iterative process

The combined results presented in this thesis suggest that the three sets of processes (niche-based processes, dispersal-based processes and abundance-based processes) can be regarded as iterative. We thus expect that the three views can reinforce each other and that their integration would increase our understanding of and ability to predict community assembly.

The potential species composition is determined by environmental conditions, acting as filters, whereas deviations from this potential composition are to a large extent determined by the degree to which seed availability is limiting (Chapters 3 and 6, Purves & Pacala 2005, Grime 2006).

The chances of propagules arriving on suitable but unoccupied habitat patches are largely determined by species-specific dispersal abilities in combination with abundance-driven, stochastic processes (Chapters 3 and 6). After the arrival of propagules at a habitat patch, their establishment success depends on the suitability of the habitat patch in terms of environmental conditions that act as a filter on germination and seedling survival.

Novel species pre-empt microsites and may influence the availability of resource levels and hence the establishment opportunities for other incoming species (Grime 1998, Davis et al. 2000, Fargione et al. 2003, Seabloom et al. 2003, Tilman 2004, Harpole & Tilman 2006). As a consequence, differences in the order of arrival of species may give rise to differences in community composition in habitat patches with similar environments (Chase 2003, Ejrnæs et al. 2006). This implies that the environmental filters on incoming propagules are in-

directly affected by dispersal processes. For established plant species, propagule output and dispersal processes for the founding of new generations are in turn influenced by resource availability and biotic interactions (Chapter 5, Bazzaz et al. 2000, Soons et al. 2004b).

From the perspective of ecosystem functioning, niche-related traits probably determine which species can potentially occur in a given habitat patch, while dispersal traits and regional abundance in the species pool determine which species actually 'do the job' (cf. Grime 2001) at local scale. In principle, ecosystem functioning might therefore be strongly affected by both seed-source limitation and dispersal limitation.



Restoration of dispersal processes in fragmented landscapes

Wim A. Ozinga

Dispersal as a key process in ecological restoration

Nature conservation projects are being carried out all over the world to maintain existing biodiversity. By contrast, ecological restoration is practised mainly in highly industrialized countries in Europe and North America (Hobbs & Norton 1996, Bakker 2005, Van Andel & Aronson 2006). Ecological restoration aims to assist the recovery of ecosystems that have been degraded, damaged or destroyed to achieve semi-natural systems in which ecological processes play a more prominent role (Hobbs & Norton 1996, Bakker & Berendse 1999, SER 2002, Van Andel & Aronson 2006).

Ecological restoration projects in Europe and North America have mainly focused on restoring abiotic conditions. Although there have been many local successes, the resulting vegetation developments in fragmented landscapes have often been disappointing, with many 'missing plant species' that had been expected to return in view of the restored environmental conditions (Dobson et al. 1997, Bekker & Lammerts 2002, Jansen et al. 2004, Walker et al. 2004, MNP 2007). In fact, such projects might even be counter-productive, since their low cost-effectiveness might reduce public support for other restoration projects.

Accumulating evidence suggests that even if abiotic conditions can be sufficiently restored, the degree to which endangered plant species re-colonize these restored areas is often small (e.g. Hutchings & Booth 1996, Bakker & Berendse 1999, Lockwood & Pimm 1999, Verhagen et al. 2001, Jacquemyn et al. 2003, Walker et al. 2004, Ozinga et al. 2005b). The availability of seeds in particular can be a major limiting factor ('seed limitation') in ecological restoration projects (Strykstra et al. 1998, Bakker & Berendse 1999, Turnbull et al. 2000, Ehrlén & Eriksson 2000, Mouquet et al. 2004, Ozinga et al. 2005a,b). For convenience we use the word seed, but it should be kept in mind that the actual dispersal unit (propagule or diaspore) can be any part of a plant, generative or vegetative, which can give rise to a new plant individual.

Metapopulation theory asserts that regional survival of species requires that local populations are connected by sufficient rates of dispersal (Levins 1969, Hanski 1998, Opdam et al. 2003). In recent years, attention has started to shift from metapopulations of single species towards so-called metacommunities (Wilson 1992, Mouquet & Loreau 2002, Leibold et al. 2004). A metacommunity can be defined as a set of local communities (with potentially interacting species belonging to the same trophic level) that are linked by the dispersal of component species. The restoration of local communities therefore requires measures to restore dispersal processes across landscapes.

Consequences of time delays in metapopulation dynamics for ecological restoration

Extinction debt: a pitfall for risk assessment

The spatial and temporal dynamics in metapopulations can greatly influence the prospects of restoration management. Metapopulation theory predicts that species can only survive at regional scale if local extinctions are compensated by an appropriate rate of colonization or recolonization of suitable habitat patches from other populations (Hanski 1998, Vos et al. 2001, Opdam et al. 2003, Holyoak et al. 2005). There are, however, considerable time delays in local extinction (Hanski 1998, Nagelkerke et al. 2002, Lindborg & Eriksson 2004, Helm et al. 2006, Vellend et al. 2006, Chapter 4). As a result, patterns in species composition are (almost) never in equilibrium with environmental conditions and habitat configuration. Instead, present-day distribution patterns of many vascular plant species may represent relicts of vanished landscapes with a higher connectivity and a more intact dispersal infrastructure. In other words: many immobile species are 'too common' for the present fragmented landscape. The spatial patterns of these species may therefore be regarded as the '*ghost of land-use past*' (cf. Harding et al. 1998, Chapter 8). In fact, many metapopulations may already have crossed the threshold value for regional extinction in the highly fragmented landscapes of industrialized countries, and these species are therefore doomed to regional extinction (Hanski 1998, Nagelkerke et al. 2002). Present-day local extinctions may thus herald larger future extinctions, unless we manage to restore the connectivity of semi-natural habitat types. This delay in extinctions has been called '*extinction debt*' (Tilman et al. 1994). The existence of many relict populations ('living dead', cf. Diamond 1991) implies the potential pitfall of underestimating the true threat status of many plant species. The results reported in Chapter 4 on aboveground survival times imply that the time delay to local extinction, and thus the possible underestimation of extinction risk, will be most pronounced in habitats with low nutrient availability and for perennial species with high abilities for clonal extension and low abilities for dispersal.

Colonization deficit: a key problem for ecological restoration

Time delays occur not only on the extinction side of the balance, but also in recolonization after de-fragmentation (Hanski 2000, Nagelkerke et al. 2002). The consequence of time delays in colonization is a slow response of many endangered species after ecological restoration. To keep up the metaphor of extinction debt, this time delay in colonization or recolonization can be termed '*colonization deficit*'. Our research revealed that the colonization deficit differs greatly between species, communities and landscapes. The time delay in colonization will be greatest for 'slow species' with low dispersal abilities (Chapters 3 and 9). The ability of these species to track suitable habitat patches is several orders of magnitude lower than that of species with high dispersal abilities (Chapter 3, Figure 10.1).



Figure 10.1: Flea Sedge (*Carex pulicaris*) is an example of a ‘slow species’ that leaves many suitable habitat patches unoccupied. *Carex pulicaris* has a very low seed production and the seeds are released over short distances with an explosive mechanism like a flea. As long-distance dispersal depends on events with a very low probability (e.g. transport by birds or by inundating water), the low seed production will strongly limit its changes in the recruitment lottery.

At landscape level, the colonization deficit is augmented by reduced numbers of seed sources in the region (Chapter 6). The increasing deficit of seeds for many endangered species in fragmented landscapes has a spatial component based on local extinctions of source populations and a temporal component based on the depletion of the soil seed banks in habitat patches that have been intensively exploited for long periods of time (Hutchings & Booth 1996, Bekker et al. 1997). In addition to the increased spatial and temporal isolation of local populations, an impoverished dispersal infrastructure will greatly reduce the rate of seed dispersal between the remaining local populations (see Chapter 8). At regional scale, it is thus a relatively small number of mobile species that dominate the landscape by their large number of individuals, while less frequent immobile and/or rare species make up the majority of species numbers and thus determine the biodiversity. The colonization deficit thus poses a key problem to restoration ecology.

Management options to mitigate the colonization deficit

In the long term, endangered, immobile plant species can only survive in fragmented landscapes if nature policy is able to increase the chances that seeds can track suitable habitat patches, i.e. to reduce the degree to which the availability of seeds forms a limiting factor. The results of our research indicate that the ability of species to track suitable habitat patches is influenced by two distinct components: (1) the relative abundance of seed sources in a given region, and (2) the actual transport of available seeds (see Chapter 9 for more details). There are therefore two principal approaches to mitigate the effects of the colonization deficit for endangered species. The first approach involves increasing the relative abundance of immobile species in the seed rain in a given landscape. The second approach involves increasing the degree of transport of available seeds by restoring dispersal processes at the landscape scale (Chapter 8). Both approaches are discussed in more detail below.

Increasing the abundance of immobile species in the seed rain in a landscape

Nature management at the landscape level has at least four options to increase the abundance of seed sources from immobile species in a given region:

1. creating new habitat patches to increase the number of potential seed sources;
2. increasing the size of relict populations as a seed source for immobile species;
3. increasing the contribution of the soil seed bank to aboveground populations by small-scale soil disturbances;
4. increasing the seed output of existing populations by varying management intensity over time.

Creating new habitat patches to increase the number of potential seed sources

In theory, creating new habitat patches can contribute to an increased availability of seed sources in the near future. Metapopulation theory predicts that even in well-connected metapopulations, suitable but unoccupied habitat patches are a common phenomenon. A strong message from metapopulation models is that from the perspective of species, even these unoccupied sites (so called ‘empty habitat patches’) can play an important part in the viability of the metapopulation as a whole (Hanski 1998, Vos et al. 2001, Opdam et al. 2003). The creation of new habitats, even though they start as empty habitat patches for most species, might thus in the longer term be useful in increasing the availability of seed sources across the landscape.

Our results imply, however, that in newly created habitat patches in fragmented landscapes, many immobile species will be highly underrepresented in comparison with habitat patches in less fragmented landscapes (Chapters 3, 6, 8). Thus, aside from the problem that many habitat types are very difficult or sometimes nearly impossible to create or to restore, this management option is not very efficient for the conservation of endangered immobile species. In fact, the creation of new habitat patches is expected to mainly benefit fast, opportunistic species with high dispersal abilities, which may subsequently reduce the accessibility of such habitat patches to immobile species by pre-empting the available microsites. The ultimate consequence of the colonization deficit for immobile species is that in fragmented landscapes it is nearly impossible to restore community types for which the targets with regard to species composition are based on historical references. This implies a strong message for land-use policy, since it means that the creation of new compensatory habitat patches as a part of integrated spatial planning (cf. Morris et al. 2006) does not offset losses of slow species, even if these new habitat patches cover much larger areas than the original habitat patches. The creation of new habitat patches as such is thus insufficient for the survival of slow species in dynamic landscapes.

Increasing the size of relict populations as a seed source for immobile species

In most fragmented landscapes in Northwest Europe, plant diversity is restricted to old landscape elements such as field margins, ditch banks, hedgerows and road verges (Smeding 2001, Geertsema 2002, Smart et al. 2002, Blomqvist et al. 2003, Weeda 2004). Old pastoral landscape elements apparently provide a refuge for many plant species from low-productive habitats that were once common in landscapes with low-intensity farming systems. Hedgerows, for example, may harbour many so-called ‘ancient forest species’ (cf. Hermy et al. 1999) as a legacy of past landscapes. These old landscape elements are especially important for species with poor dispersal abilities, since such immobile species cannot track the modern-day human-induced landscape dynamics with its high turnover rate of habitat patches (Chapter 3).

After local habitat deterioration, many plant species can persist for a long time by clonal growth, despite the fact that environmental conditions have become less suitable, leading to so-called ‘remnant populations’ (Eriksson 1996). This delay in extinction can be used to our advantage in restoration management at the landscape scale. Although these remnant populations are often relatively small, they may function as important seed sources for the restoration of habitat patches embedded in agricultural landscapes (e.g. Bossuyt et al. 1999, Opdam et al. 2001, Petit et al. 2004, Honnay et al. 2005, Grashof-Bokdam & Van Langevelde 2005). These remnant populations can be regarded as a kind of ‘external ecological memory’ of past landscapes (cf. Bengtsson et al. 2003).

Conservation and restoration of old landscape elements with remnant populations might therefore be regarded as a form of insurance for the maintenance of

biodiversity in agricultural landscapes. Increasing habitat quality in the immediate vicinity of these old habitat patches is probably an efficient way to increase the abundance of seeds (propagules) of 'slow species' in the regional species pool of fragmented landscapes.

Increasing the contribution of the soil seed bank to aboveground populations by small-scale soil disturbances

For plant communities with a high proportion of species with persistent seeds in the soil seed bank, the soil can be regarded as a kind of '*internal ecological memory*' of past community types (cf. Bakker et al. 1996, Bengtsson et al. 2003). For many species with the ability to accumulate a persistent seed bank, small-scale disturbances of the soil profile might trigger germination. The accumulation of a persistent soil seed bank enables these species to bridge periods of unsuitable environmental conditions. This buffering effect can be regarded as a so-called '*storage effect*' (cf. Chesson & Huntly 1989, Levine & Rees 2004) because the local persistence of populations at a given habitat patch relies not only on the aboveground vegetation but also on the storage of reproductive potential in the soil until conditions become more suitable again. Indeed the results from Chapter 8 showed that the ability to accumulate a persistent seed bank strongly reduces the risk on decline across the 20th century.

Although the germination of most species may benefit from the creation of gaps, it is especially small-seeded species with a persistent seed bank which depend on such gaps (Gross & Werner 1982, Thompson & Baster 1992, Baskin & Baskin 1998, Fenner & Thompson 2005). Temporal variations in environmental conditions have traditionally been regarded as a threat to the persistence of endangered plant species (Lande 1988, Menges et al. 2000). The fact that many endangered plant species with a persistent seed bank depend on small scale disturbances, however, suggests that these species in fact benefit from intermediate levels of temporal variation in environmental conditions (Higgins et al. 2000, Levine & Rees 2004).

In the present-day European and North American landscapes, natural dynamics have been severely reduced and replaced by new types of human-induced disturbances (Pickett & Thompson 1978, Dale et al. 1998, Turner et al. 1998, Bengtsson et al. 2003). As a consequence, the disturbance regime may no longer be appropriate for the regional survival of a subset of the habitat species pool. In some cases, this mismatch between the disturbance regime within nature reserves and the germination niches (cf. Grubb 1977) of endangered species might be resolved by recreating larger, more dynamic nature reserves, e.g. in some river valleys. The vast majority of nature reserves will, however, be simply too small and too static to allow an appropriate disturbance regime. In these remaining reserves, the triggering of the soil seed bank will therefore depend on human-induced disturbances that imitate natural disturbance regimes.

Our knowledge of the germination niche is incomplete for many endangered species. In addition, recruitment opportunities for several endangered plant

species are probably rare and episodic even under natural disturbance regimes (Crawley 1990, Rackham 1998, Eriksson & Froberg 1996, Young et al. 2005) and for these species, the required disturbances may be difficult to mimic by humans. Since there are many factors that determine variation in germination across species (Grubb 1977, Fowler 1988, Baskin & Baskin 1998, Fenner & Thompson 2005), the challenge to nature managers will be to find out what kind of disturbances are needed to trigger the germination of seeds from endangered species, and what environmental conditions are needed for subsequent survival. The fine-tuning of such management practices therefore requires experienced local managers with a highly developed intuition for the specific requirements.

There are many examples from the Netherlands in which triggering of the soil seed bank by small-scale soil disturbances has indeed resulted in recolonizations after decades of absence. This concerned not only rare arable weeds, but also endangered species from grasslands and fens such as *Anagallis tenella*, *Apium repens*, *Carex hostiana*, *C. pallescens*, *Cicendia filiformis*, *Centaureum pulchellum*, *Hypericum montanum*, *Juncus alpinoarticulatus*, *J. capitatus*, *J. pygmaeus*, *J. tenageia*, *Lobelia dortmanna*, *Ludwigia palustris*, *Pinguicula vulgaris*, *Scutellaria minor* and *Viola persicifolia* (Salisbury 1952, 1961, Jansen et al. 2000, Weeda 2001, 2000-2005, Grootjans et al. 2002, Roelofs et al. 2002, Matus et al. 2003, Van Beers & Weeda in press).

On the other hand, human-induced small-scale soil disturbances may also have unintended negative effects. In the first place, triggering seed germination at the wrong moment (i.e. when environmental conditions are not yet suitable) can have an adverse effect since this depletes the soil seed bank (Bakker et al. 1996, Roelofs et al. 2002). In the second place, small-scale disturbances of abandoned agricultural grasslands might lead to the dominance of competitive species with a persistent seed bank such as *Juncus effusus*, *Ranunculus repens* and *Rumex crispus* (Bekker et al. 1997, Verhagen et al. 2003), reducing the availability of suitable microsites for the establishment of less competitive endangered species. In Northwest Europe, *Juncus effusus* for example has become dominant on many abandoned moist grasslands with a low-intensity grazing management (Richards & Clapham 1941, Lamers et al. 2006).

Stimulating germination from the soil seed bank is only a reliable management option for species with the ability to accumulate a persistent soil seed bank, and for habitat patches in which these species used to occur in the past and that have not been exploited too intensively by modern agriculture. Grasslands that have been ploughed and fertilized for extended periods of time virtually lack any viable soil seed banks of 'target species' from former grassland communities (Hutchings & Booth 1996, Bekker et al. 1997, Bakker & Berendse 1999). In short, the restoration of many habitat types in fragmented landscapes cannot rely on the presence of many endangered plant species in the seed bank. Therefore restoration success depends to an important degree on the availability of aboveground seed sources nearby.

Increasing the seed output of existing populations by varying management intensity over time

DILEMMA BETWEEN NICHE-BASED AND DISPERSAL-BASED MANAGEMENT

The management of well developed, species rich vegetations may also require some adjustments in order to increase the efficiency of the available populations to act as a seed source. Management measures aiming to reduce nutrient availability in eutrophicated habitat patches, such as grazing and cutting, may at the same time prevent seed set by many grassland species (Coulson et al. 2001, Pywell et al. 2003). As a result, the presence of certain plant species in the regional species pool does not guarantee that these species are represented in the seed rain. At larger spatial scales, management practices that reduce seed production therefore decrease the probability of colonization of unoccupied habitat patches in the surroundings, which may slow down metacommunity dynamics. At local scale, this may give rise to a dilemma between niche-based management and dispersal-based management.

The paramount importance of seed-source limitations for community assembly documented in this thesis challenges nature management to find a new balance between management measures that optimize the reduction of nutrient availability (e.g. early cutting or cutting twice) and measures that allow appropriate seed production by endangered plant species (e.g. late cutting). The following section provides some suggestions to increase the production and release of ripe seeds within several management regimes. The general suggestion is that the key mechanism is to allow greater temporal dynamics or to vary management intensity over space and time.

RELEASE FROM GRAZING PRESSURE

At the landscape scale, nature management by introducing large herbivores has become common practice in large parts of Europe (Bakker & Berendse 1999). This includes the introduction or reintroduction of wild herbivores as well as the introduction of 'primitive' or de-domesticated livestock breeds (Figure 10.5 and 10.6). Without human interference, animal numbers in Northwest-European ecosystems are mainly regulated by the limited food availability in the winter period. In the summer period, there is a surplus of food, leading to the development of temporarily ungrazed areas covered by vegetation with a lower nutritional quality (e.g. Wallis de Vries 1995, Hobbs 1996, Olff et al. 1999, Bakker et al. 2004), allowing the production of ripe seeds. Parts of these areas are grazed during the winter, in periods of food shortages. In addition to seasonal variations in grazing pressure, near-natural ecosystems are also characterized by large year-to-year fluctuations in grazing pressure (Olff et al. 1999). These spatial and temporal variations in grazing pressure may lead to shifting mosaics of grasslands, fringes, mantles with spiny shrubs and closed forests (Watt 1947, Remmert 1991, Vera 2000, Olff et al. 1999). Vera (2000) therefore proposed 'naturalistic grazing' with free-moving large herbivores as a way to create and maintain these shifting mosaics.

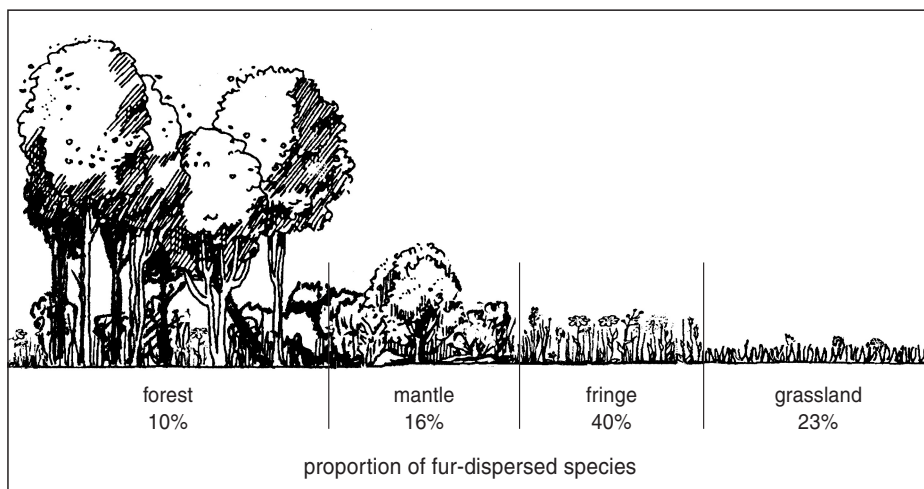


Figure 10.2: Transect from forest through mantle and fringe vegetation to grassland. The percentages represent the proportion of endangered plant species that can be effectively dispersed in the fur of mammals (based on data from Ozinga et al. 2004).

In grazed landscapes, a relatively high proportion of endangered grassland plants probably depend on periods of low grazing pressures or on fringes with unpalatable ‘nurse species’ for the production of ripe seeds. When we analyzed dispersal traits across community types, it became apparent that the plants with a high ability for fur-assisted dispersal occurred mainly in fringes (Figure 10.2). Since this group of plant species has shown a severe decline over the 20th century in Northwest Europe, this result underlines the importance of spatial and temporal variation in grazing pressure for the regional survival of these species.

There is, however, considerable debate on the question whether naturalistic grazing in itself (without human interference) is able to create and maintain such vegetation mosaics with fringe vegetations in fragmented landscapes without natural disturbance regimes (e.g. Sutherland 2002, Svenning 2002, Bradshaw et al. 2003, Mitchell 2005). Regardless of this debate, naturalistic grazing is only feasible in regions that harbour very large nature reserves.

By contrast, in many small and fenced nature reserves (<50 ha), the stocking densities are determined by humans and are mainly based on the biomass production during the summer season in order to reduce nutrient availability. This leads to much higher stock densities than in naturalistic grazing, preventing the production of ripe seeds by many plant species (Coulson et al. 2001, Pywell et al. 2003, personal observations). Periodic release from grazing pressure over time (intermittent grazing) is therefore required to increase the proportion of plants that manage to release seeds.

More variation in grazing pressure in small nature reserves can be achieved by rotational grazing using spatial and temporal variations as regards rotation times (Morris 2000, Dolek & Geyer 2002) or by short-duration grazing at high stock densities. There is also another reason why short-duration grazing at high stock densities might be advantageous for species diversity. Herbivores at high stock densities may learn to mix plants in their diets that differ in terms of the types and concentrations of secondary metabolites (Provenza et al. 2003, Villalba et al. 2004, Villalba & Provenza 2005). This mixing of plant species can probably be explained by the fact that different secondary plant metabolites are likely to be less toxic as a diluted mixture (Freeland & Janzen 1974, Villalba & Provenza 2005; Ozinga unpubl. data; Figure 10.3). More varied diets promote a more uniform use of plant species within the community, enabling palatable species to maintain higher abundances (Provenza et al. 2003) and to produce seeds. Since the species-specific ability to be dispersed by the dung of large mammalian herbivores is generally positively related to the palatability of the foliage (Janzen 1984, Durka & Ozinga in prep.), this may increase the diversity of plants that can be dispersed by dung.

In small, fenced nature reserves, it might be worthwhile to periodically prevent grazing during the summer season and to allow grazing in the autumn and winter season. Superimposed on this temporal variation, the spatial variation in small areas can be increased by periodically setting up movable exclosures.

HAYMAKING AND DISPERSAL PHENOLOGY

Management by cutting and removing hay is another important tool in counteracting the effects of eutrophication (Olff & Bakker 1991, Bakker & Berendse 1999). In large parts of Northwest Europe, management by haymaking has become rather intensive, using large machinery and with little spatial and year-to-year variation in the timing of mowing. An important drawback of this intensive haymaking, in parallel with grazing, is that it can hamper the production and release of ripe seeds by late-flowering species. Since many grassland plants have a high aboveground persistence (see Chapter 4), a delay of mowing once in the few years might already be sufficient for a substantial increase in seed output. More variation in mowing dates may also be advantageous for the subsequent seed dispersal. Mowing machinery itself can be an efficient transport vector for seeds (Strykstra et al. 1997) and a larger variation in mowing dates might therefore allow a wider spectrum of species to be transported.

Hay meadows might also profit from incidental grazing at the end of the growing season. Although many species which are regarded as characteristic 'hay meadow species' are sensitive to grazing in the growing season, incidental grazing at the end of the growing season can facilitate seed dispersal and can create 'windows of opportunity' for the germination of subordinate species. Many hay meadow species occur in more natural landscapes in forest mantles, fringes and other parts with a low food quality that are only grazed in periods of low food supply at the end of the growing season (Ellenberg 1988).



Figure 10.3: Ancient sheep breeds like Gotland Pelt sheep (upper panel, with natural moulting of the fleece), Scottish Blackface (lower panel) and Drenthian heather sheep can better cope with plant species with high concentrations of secondary metabolites as compared to more domesticated breeds. Short-duration grazing with these breeds at high stock densities leads to more varied diets which in turn increases the diversity of plant species that can be dispersed by dung and at the same time enables palatable plant species to maintain higher abundances.

RECONCILING NICHE-BASED MANAGEMENT AND DISPERSAL-BASED MANAGEMENT IN ECOLOGICAL RESTORATION

In conclusion, it is suggested that in semi-natural landscapes, the long-term survival of many grassland species might depend on periodic release from intensive management. With regard to both seed dispersal and germination, it is not the mean values of management regimes that are important, but the spatial and temporal variations around the mean.

A disadvantage of the suggested temporary release from intensive management is that this might in the short term lead to increased accumulation of litter and aboveground biomass and a subsequent loss of species with low competitive abilities (Bakker et al. 2002, Schaffers 2002). High aboveground biomass and litter accumulation may hamper the recruitment of species in unoccupied but suitable habitat patches by preventing seed deposition, germination or seedling survival (Grime 2001, Wilson & Tilman 2002, Stevens et al. 2004). In effect, these processes isolate highly productive habitat patches from propagules that are available in the regional pool.

If such a release from intensive management is applied at low frequency and on small and shifting parts of the area, the negative effects of temporarily increased litter accumulation on restoration success are probably relatively small (cf. Bakker et al. 2002), while the ecological gain of such release from intensive management is expected to be relatively large. There is some evidence that for many perennial grassland species, regeneration is an episodic process with long periods lacking any regeneration (Grubb 1977, Rackham 1998, Eriksson & Froberg 1996). For these species a slight increase in the spatial and temporal variation in management intensity might already be sufficient for their regional survival. On the other hand, the conservation of species that are short-lived and which lack a persistent seed bank, may require a stronger increase in the frequency of release from the management regime. Information on life-history traits of species within a given ecosystem or landscape can be used as a clue for adjusting the frequency, timing and spatial scale of current management practices. The optimal frequency of release from intensive management will depend on habitat type and landscape characteristics, and again requires experienced local managers with a highly developed intuition for the specific requirements.

Restoring the dispersal infrastructure

The second set of measures to reduce the degree of seed limitation is the restoration of dispersal processes at landscape scale. An important result of the present research is that differences between species in terms of adaptations to various dispersal vectors are a key factor in explaining losses of plant diversity in Northwest Europe in the 20th century, with water- or fur-assisted dispersal being over-represented among declining species, while others (wind- or bird-assisted dispersal)

are under-represented (Chapters 8 and 9). We found that, contrary to common belief, changes in the availability of dispersal vectors (dispersal infrastructure, see Box 3) are as important as the more commonly accepted changes in habitat quality in explaining plant diversity losses. The impoverished dispersal infrastructure limits the effectiveness of the regional species pool as a seed source for local colonization. Hence, our findings call for measures to restore the dispersal infrastructure across entire regions, which go beyond current conservation practices.

The creation of large ecological networks of nature reserves, such as the EU's prestigious and costly Nature 2000 framework and the Pan-European Ecological Network, is being proposed as a tool to mitigate the effects of habitat fragmentation and to enhance the rate of dispersal between habitat patches (Council of Europe 2000). Although these ecological networks are mainly designed for the dispersal of large animal species, they are also expected to function as corridors for plants. There have, however, been surprisingly few empirical studies of the effectiveness of ecological corridors for the dispersal of plant species. Our findings in fact suggest that the creation of static networks as such is probably not enough to halt the loss of plant diversity, since many plants need mobile dispersal vectors such as running water and free moving or herded mammals or birds ('moving corridors'; Poschlod et al. 1996, Lundberg & Moberg 2003). Trait spectra at the community level (cf. Chapter 5) can provide some guidance for the kind of dispersal vectors that have to be restored to maintain and restore plant diversity. The following options may play a vital role in improving the diversity of dispersal opportunities for endangered plant species and thus increase the effectiveness of the regional species pool as a seed source for local colonization:

- 1) River rehabilitation projects (allocating more space to rivers and brooks).
- 2) Robust ecological networks for large mammals.
- 3) Reinforcement of low-input farming systems.

Allocating more space to rivers and brooks

The efficiency of water as a vector for lateral and longitudinal seed dispersal can probably be increased by rehabilitation projects which allocate more space to rivers and brooks. Such projects are expected to lead to more natural flooding dynamics in terms of magnitude, frequency, duration and timing (flood-pulse concept, cf. Tockner et al. 2000), which in turn may lead to enhanced seed dispersal (Jansson et al. 2000, 2005, Boedeltje et al. 2004, Van Eck et al. 2005, Nilsson et al. 2005, Leyer et al. 2006).

More natural flooding regimes are not only profitable for the dispersal of aquatic or semi-aquatic species (e.g. Boedeltje et al. 2004) but also for that of species from drier habitats within the reach of occasional inundations. An intriguing result reported in Chapter 8 is that among the species with floating seeds, the



Figure 10.4: Allocating more space to rivers and brooks in order to allow more natural flooding regimes (including inundations) is profitable for the exchange of floating propagules between sites. This example shows an inundation in the IJssel valley with flowers of British Fleabane (*Inula britannica*). The propagules of this species have a pappus of fine hairs, but in the Netherlands most seeds are not viable and their dispersal mainly depends on floating root fragments which are transported by inundating water during autumn and winter (Photo R. Knol).

greatest declines were observed among those characteristic of relatively dry soils in the higher parts of floodplains. This emphasizes the importance of the conservation or development of high-elevation river dunes in riverine landscapes. Although winter inundations of high-elevation areas might be very sporadic and short, their impact on colonization probabilities and hence on local species composition is probably high (cf. Ozinga et al. 2004, Van Eck 2004; Figure 10.4).

Allocating more space to rivers and brooks by re-establishing floodplains (i.e. relocating dikes further from the river or brook) is not only beneficial for plant dispersal but may also reduce flooding risks. Recent views recognize the major drawbacks of river regulation, which results in larger water level fluctuations and high flood peak discharges (Nienhuis & Leuven 2001). This radical shift in hydrological management practice is apparently accelerated by the recent severe flood events in Central Europe and by the results of climate change models that suggest that episodes of severe flooding may become more frequent in Europe (Christensen & Christensen 2003). Decision makers in Europe now increasingly recognize that rivers and brooks should be allowed to have a more natural flooding regime and to occupy more natural potential space (Nienhuis & Leuven 2001).

Successful examples of the large-scale restoration of environmental conditions relate mainly to dynamic parts of large rivers such as the Rhine and Meuse (Peters 2000, 2004, Weeda et al. 2000-2005), while the successes for less dynamic parts and smaller river- and brook valleys seem more limited (Weeda et al. 2000-2005, 2006, Lamers et al. 2006).

Robust ecological networks for large mammals

Ecological networks such as the Pan-European Ecological Network may enhance the exchange of the remaining large mammals between nature areas (Council of Europe 2000, Van Opstal 2000). For many species, the retention time of seeds in large mammals (both externally in the fur and internally in the digestive tract) is long enough to enable seeds to be transported across corridors over distances of many kilometres (Fischer et al. 1996, Pakeman 2001, Cosyns 2004, Couvreur et al. 2004, Mouissie 2004, Myers et al. 2004, Römermann et al. 2005, Manzano & Malo 2006).



Figure 10.5: The European Bison (*Bison bonasus*) is one of the last remaining mega-herbivores in Europe which was recently introduced in a few Central European nature reserves (photo G. Pohl). The species has a different habitat use and feeding behaviour as compared to Cattle and Horse and is better equipped for foraging in forests. It can therefore fulfil a complementary role in seed dispersal. Sustainable populations however require very large nature reserves (individual home range 500-1500 ha).

In order to be effective for a wide range of taxonomic groups, ecological networks should therefore be robust in the sense that they are not too narrow (at least 1 km on average) and have a high spatial cohesion of various habitat types (robust ecological networks cf. Opdam et al. 2003).

For mammals with a large home range (which are probably the most efficient vectors for long-distance seed dispersal, see Figure 10.5 and 10.6), the spatial planning and the actual construction of such robust ecological networks appears to be complicated by many conflicts of interest (Wallis de Vries 1995, Opdam et al. 2002). Groot Bruinderink et al. (2003) used a landscape-ecological metapopulation model to assess the sustainability of habitat networks for metapopulations of large mammals in Northwest-Europe, using Red deer (*Cervus elaphus*) as a kind of flagship species. They concluded that apart from a few large forest areas, existing or potential populations are embedded in poorly connected landscapes. This poor connectivity reduces the chances of long-distance seed transport by large mammals to almost zero.



Figure 10.6: Naturalistic grazing with Galloway Cattle along the Rhine near Millingen with propagules of Burdock (*Arctium spec.*) attached to the fur (Photo E. Hazebroek). Large river valleys provide good opportunities for the development of robust ecological networks with naturalistic grazing. Cattle breeds with a rough fur are more efficient for the transport of seeds through attachment as compared to breeds with a more sleek short-haired fur.

Although ‘naturalistic grazing’ in nature reserves (cf. Vera 2000), combined with the creation of ecological networks between these reserves can be a very valuable management option, it is mainly effective for the regional conservation of plant diversity in regions that still harbour large nature reserves. This leaves large stretches of land in Northwest Europe where other (complementary) management alternatives might be more suitable. From a plant perspective, this implies that the creation of ecological networks, although very valuable, will on its own not be sufficient for the conservation and restoration of plant diversity. This stresses the importance of complementary approaches such as reinforcement of low-intensity livestock systems. In effect, these complementary approaches should increase the rate of seed dispersal in the landscape between the corridors. Or to put it in terms of metacommunity theory: additional measures need to increase the ‘permeability’ of the matrix landscape between the habitat islands. This is a crucial yet often overlooked issue in restoration ecology.

Reinforcement of low-input farming systems

The observed impact of changing livestock systems on plant diversity losses in Northwest Europe (Chapter 8) emphasizes the importance of low-input farming systems with free-ranging or herded livestock for long-distance seed dispersal, and hence for the regional survival of plant species. The key message is therefore that the long-term survival of many grassland species in currently fragmented landscapes will critically depend on the reinforcement of low-input farming systems, including herded and / or free-ranging livestock on common grounds (Figure 10.7).

Despite their ecological importance, low-input farming systems are vanishing across Europe. This is largely a result of polarization of land use with intensified use on the one hand and abandonment of traditional agricultural practices on the other (Vos & Stortelder 1992, Bignal & McCracken 1996, Luick & Bignal 2002). For the coming decades, it is expected that traditional agriculture will no longer be economically profitable on 70% of the present agricultural land in the EU (Rural European Platform 2006). Acknowledgement of the important role of low-intensity grazing systems for the maintenance of species-rich grasslands and wooded meadows should lead to a re-valuation of pastoral systems. The remaining areas with free-ranging or herded livestock and high biodiversity should not necessarily be viewed as an archaic remnant of the past but instead can be regarded as a basis for future sustainability, and should therefore be encouraged.

This does not necessarily imply that old farming systems need to be restored in every detail. If they do not provide economic value on the local or regional market, such systems will not be sustainable (Costanza et al. 1997, Carpenter et al. 2001, Stortelder et al. 2001, Rosenzweig 2003, Adams 2006, Schrijver et al. 2007). The challenge will be to develop new varieties of traditional farming systems that meet modern criteria with regard to biodiversity and socioeconomic sustainability.



Figure 10.7: Directed seed dispersal with a herded sheep flock (shepherd being assisted by a working sheep dog). In strongly fragmented landscapes grazing by herded livestock with well-planned rotation schemes is probably more effective for seed transport of endangered species as compared to free ranging livestock.

From an ecological point of view, the efficiency of agri-environmental schemes might be greatly increased if the system were able to combine metacommunity processes with the socio-economic context of current farming systems. This might be achieved by spatially clustering agri-environmental schemes and by allowing longer time frames (Stortelder et al. 2001, Kleijn et al. 2006). Another, more flexible, possibility is the concept of ‘farming for nature’ (Stortelder et al. 2001, Schrijver et al. 2006, 2007). In this approach, the ecological and economic sustainability of pastoral systems for local farmers is increased by payments for integrated, low-input farm systems within a region. Thanks mainly to the larger spatial and temporal scales and the lower fixed assets, ‘farming for nature’ is probably a more cost-effective way to increase or maintain plant diversity than traditional agri-environmental schemes.

With regard to seed dispersal across landscapes, our results indicate that it is crucial (1) to focus on areas that still harbour enough source populations, (2) to increase the range of plant species that can release ripe seeds by varying management intensity over space and time, and (3) to improve the dispersal infrastruc-

ture between individual fields. These three goals might be achieved in the ‘farming for nature’ approach by ensuring that these integrated farm systems cover large spatial and environmental gradients including nature reserves and common grounds for low-intensity livestock grazing. Since governments in the European Union spend roughly 35 billion a year on agri-environmental schemes that cover a quarter of farmland in the EU (Whitfield 2006), there is a need to consider the role of seed dispersal in the evaluation of various land-use scenarios.

Last option at the species level: re-introduction

Rarity in itself may increase the risk of local extinction due to stochastic processes (Gilpin & Soulé 1986, Nee & May 1997, Hubbell 2001, Chapter 8). For some endangered species, which have become very rare in the regional species pool and have low dispersal abilities, the above management options at the landscape level might therefore not be sufficient to prevent regional extinction. For these species, some form of management at the species level may be required, which may include conscientious but deliberate re-introduction schemes. Re-introduction may be approached by indirect methods (e.g. by spreading hay from donor sites containing target species) or by direct sowing or even planting of plants that are pre-grown in the greenhouse. The disadvantage of planting is that environmental filters do not select the individuals that are adapted to local conditions. This strategy may therefore be restricted to species that are endangered worldwide (IUCN 1998). Sowing with seed mixtures is a cost-effective method for diversifying impoverished local plant communities, provided that suitable microsites for establishment are available (Walker et al. 2004).

Guidelines for re-introduction strategies have been formulated by Bullock & Hodder (1997), IUCN 1998, Van Groenendael et al. 1998, Strykstra (2000) and Vergeer (2005). According to the IUCN (1998), the feasibility of re-introduction projects should be checked in advance by a multi-disciplinary population and habitat viability analysis. Such a study should not only include local habitat conditions, but also the availability of dispersal mechanisms (Chapter 8) and biotic interactions. Although the present work focused on vascular plants, it should be remembered that there may be indirect effects of fragmentation that are mediated by changes in species composition at other trophic levels, such as mycorrhizal fungi (Grime et al. 1987, Ozinga et al. 1997, Van der Heijden et al. 1998), soil invertebrate fauna (De Deyn et al. 2003) and pollinators (Kearns et al. 1998).

Since functional traits have predictive power for community assembly (Chapter 9) and for assessing which species are most at risk in fragmented landscapes with an impoverished dispersal infrastructure (Chapter 8), the importance of knowledge about functional attributes of individual plant species can hardly be overestimated in designing restoration or re-introduction programmes. Table 10.1 presents an overview of plant characteristics that can be used to assess the urgency

of re-introduction. Within individual countries, priority should be given to species that are under threat in large parts of their entire geographical range (IUCN 1998). For Northwest European countries, this is only a small subset of the species included in national Red Lists (Ozinga & Schaminée 2005).

Re-introduction is not without its critics, both on scientific and ethical grounds. From an ethical point of view, several authors argue that the chances in the 'recruitment lottery' (and hence the local species composition) are being manipulated by 'cheating' (Westhoff 1994, Weeda 1997). From a scientific point of view, the possible effects of re-introduction on the genetic variation of relict populations may be an important risk factor. When seeds from maladapted populations are introduced in a region with locally adapted relict populations, this may lead to a dilution of the locally adapted genotypes, resulting in reduced plant fitness (outbreeding depression; Rhymer & Simberloff 1996, Montalvo & Ellstrand 2001, Vergeer et al. 2004). This genetic risk may be reduced by introducing seeds from large numbers of unrelated individuals, from which the best adapted individuals are subsequently filtered by local environmental conditions (Tecic et al. 1998, Vergeer et al. 2005). In addition, the introduction of genetically uniform populations may lead to lower levels of genetic variation within the region and to reduced plant fitness (inbreeding depression; Charlesworth & Charlesworth 1987, Vergeer et al. 2004, Ouborg et al. 2006). Re-introduction therefore requires proper monitoring.

Another risk factor that becomes apparent from the present research (Chapter 8) is that re-introduction might lead to a far too optimistic view of the percentage of endangered plant species. Re-introductions of endangered immobile species in highly fragmented landscapes will not lead to sustainable populations if the rate of seed dispersal remains insufficient and if the metapopulation still remains below the threshold value for metapopulation extinction (Tilman 1994, Hanski 1998, Nagelkerke et al. 2002). Re-introductions may therefore distract attention from the fundamental problem of habitat fragmentation in combination with an impoverished dispersal infrastructure.

Table 10.1: Species characteristics that can be used to assess the urgency of additional species management. The larger the number of 'no' answers to the questions, the greater the vulnerability to habitat fragmentation and the urgency for additional species level management (*: plant property discussed in more detail in this thesis).

Species present in regional habitat species pool?*	Yes / No
Species with many small seeds?*	Yes / No
Species with high potential for long-distance dispersal?*	Yes / No
Species with more than one long-distance dispersal vector?*	Yes / No
Long-lived species with many reproductive seasons?*	Yes / No
Species with persistent seed bank?*	Yes / No
Species with mechanisms reducing inbreeding risks?	Yes / No

Improving the efficiency of ecological restoration through monitoring

Various restoration measures are likely to differ in the degree to which they increase the efficiency of seed dispersal. This will probably depend not only on inherent differences in the measures themselves but also on the spatial and historical context. Due to a serious lack of appropriate monitoring of the efficiency of restoration measures in Europe (cf. Sutherland et al. 2004) there are hardly reliable comparative data available to address this important issue. Coordinated monitoring programmes are therefore a prerequisite to improve the efficiency of restoration projects.

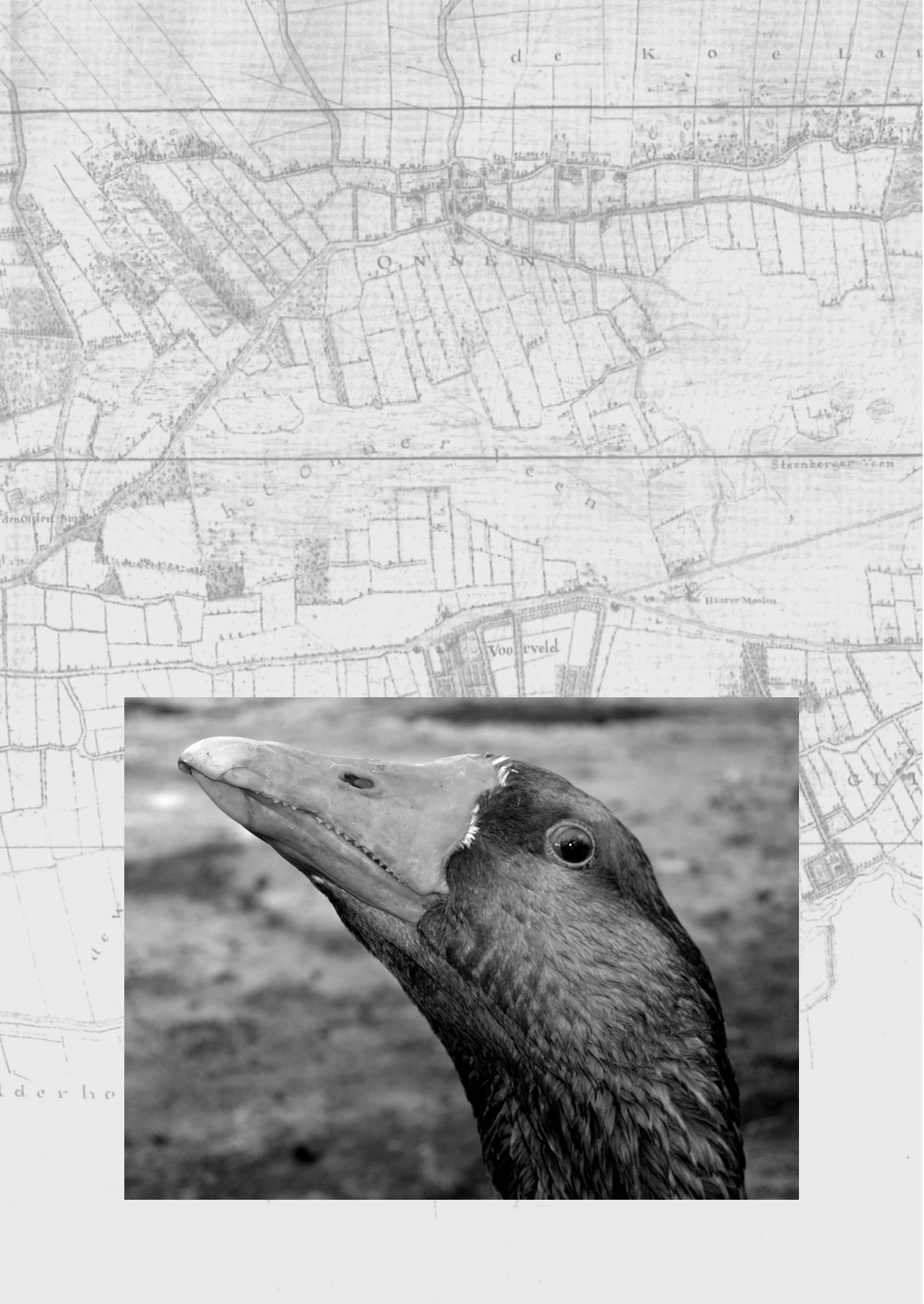
The proper evaluation of habitat restoration projects in turn requires the setting of structural and functional targets, as well as knowledge about the feasibility of these targets (Schemske et al. 1994, Hobbs & Norton 1996; Bakker & Berendse 1999, Berendse et al. 2004). In the Netherlands, for example, 'target communities' have been formally described in terms of habitat characteristics and a set of characteristic 'target species' (Bal et al. 2001, Bakker 2005), and a compa-



Figure 10.8: Local managers of small nature reserves can in many cases not be blamed for the absence of 'target species' with low dispersal abilities, such as *Gagea spathacea*, if these species are rare in the regional species pool and if the dispersal infrastructure is impoverished. The conservation of endangered species with low dispersal abilities requires the restoration of dispersal processes at the regional scale.

rable system has been developed in the European Union as a framework for Natura 2000 (European Commission 2003). The comparison of locally assigned target communities with the actual results can help to adjust restoration efforts and management regimes.

In several European countries (e.g. the Netherlands) the government compensates management costs based on the fulfilment of the targets within a given period. The low predictability of local species composition due to dispersal limitation (Ozinga et al. 2005b, Chapter 9) sets severe limits on the usability of the concept of target communities for the payment of local management. Managers of small nature reserves can in many cases not be blamed for the absence of target species with low dispersal abilities if these species are rare in the regional species pool and if the dispersal infrastructure is impoverished (Figure 10.8). The conservation of endangered species with low dispersal abilities requires an appropriate land-use policy at the regional scale.



References

- Abrams, P.A. 2001. A world without competition. *Nature* 412: 858-859.
- Ackerly, D.D. 2003. Community assembly, niche conservatism, and adaptive evolution in changing environments. *Int. J. Plant Sci.* 164: 165-184.
- Adams, W.M. 2006. *The future of sustainability: Re-thinking environment and development in the twenty-first century*. IUCN.
- Adler, P.B., J. HilleRisLambers & J.M. Levine. 2007. A niche for neutrality. *Ecol. Lett.* 10: 95-104.
- Aerts, R. & Bobbink, R. 1999. The impact of atmospheric nitrogen deposition on vegetation processes in terrestrial, non-forest ecosystems. *The impact of nitrogen deposition on natural and semi-natural ecosystems* (ed. by S.J. Langan), pp. 85-122. Kluwer, Dordrecht.
- Agnew, A.D.Q & Flux, J.E.C. 1970. Plant dispersal by hares (*Lepus capensis*). *Ecology* 51: 735-737.
- Alonso, D., R.S. Etienne & J. McKane. 2006. The merits of neutral theory. *Trends Ecol. Evol.* 21: 451-457.
- Andersen, M.C. 1991. Mechanistic models for the seed shadows of wind dispersed plants. *Am. Nat.* 137: 477-497.
- Andersen, M.C. 1992. An analysis of variability in seed settling velocities of several wind-dispersed Asteraceae. *Am. J. Bot.* 79: 1087-1091.
- Anderson, L.L., F.S. Hu, D.M. Nelson, R.J. Petit & K.N. Paige 2006. Ice-age endurance: DNA evidence of a white spruce refugium in Alaska. *Proc. Natl. Acad. Sci. U.S.A.* 103: 12447-12450.
- Andersson, E. & Nilsson, C. 2002. Temporal variation in the drift of plant litter and propagules in a small boreal river. *Freshwater Biol.* 47: 1674-1684.
- Andersson, E., Nilsson, C. & Johansson, M.E. 2000. Plant dispersal in boreal rivers and its relation to the diversity of riparian flora. *J. Biogeogr.* 27: 1095-1106.
- Askew, A., Corker, D., Hodkinson, D.J. & Thompson, K. 1997. A new apparatus to measure the rate off fall of seeds. *Funct. Ecol.* 11: 121-125.
- Augsburger, C.K. & Franson, S.E. 1987. Wind dispersal of artificial fruits varying in mass, area and morphology. *Ecology* 68: 27-42.
- Augsburger, C.K. 1986. Morphology and dispersal potential of wind-dispersed diaspores of neotropical trees. *Am. J. Bot.* 73: 353-363.
- Austin, M.P. 2005. Vegetation and environment: discontinuities and continuities. In: E. van der Maarel (Ed.): *Vegetation Ecology*, pp. 52-84. Blackwell Publishing.
- Austin, M.P., Nicholls, A.O. & Margules, C.R. 1990. Measurements of the realized qualitative niche: environmental niches of five Eucalyptus species. *Ecol. Monogr.* 60: 161-177.
- Baaijens, G.J., F.H. Everts & A.P. Grootjans. 2001. Traditionele bevoeiing van grasland. *OBN rapport* 18. Expertisecentrum LNV, Ministerie van LNV. [In Dutch].
- Baillie, J.E.M., Hilton-Taylor, C & Stuart, S.N. 2004. *2004 IUCN Red List of threatened species. A global species assesment*. IUNC, Gland, Switzerland and Cambridge. 191 pp.
- Bakker, E.S. & Olff, H. 2003. Impact of different-sized herbivores on recruitment opportunities for subordinate herbs in grasslands. *J. Veg. Sci.* 14: 465-474.
- Bakker, E.S., H. Olff, C. Vandenberghe, K. De Maeyer, R. Smit, J.M. Gleichman & F.W.M. Vera. 2004. Ecological anachronisms in the recruitment of temperate light-demanding tree species in wooded pastures. *J. Appl. Ecol.* 41: 571-582.
- Bakker, J.P. & F. Berendse. 1999. Constraints in the restoration of ecological diversity in grassland and heathland communities. *Trends Ecol. Evol.* 14: 63-68.
- Bakker, J.P. & Olff H. 1995. Nutrient dynamics during restoration of fen meadows by haymaking without fertiliser application. In: Wheeler B.D., Shaw S.C., Foit W.J. & Robertson R.A. (eds.), *Restoration of temperate wetlands*. pp. 143-166. Wiley, Chichester
- Bakker, J.P. 1989. *Nature management by grazing and cutting*. Kluwer Academic Publishers, Dordrecht.
- Bakker, J.P. 2005. Vegetation conservation, management and restoration. In: E. van der Maarel (Ed.): *Vegetation Ecology*, pp. 309-331. Blackwell Publishing.
- Bakker, J.P., Grootjans, A.P. Hermy, M. & Poschlod, P. 2000. How to define targets for ecological restoration? - Introduction. *Appl. Veg. Sci.* 3: 3-6.
- Bakker, J.P., Olff, H., Willems, J.H. & Zobel, M. 1996. Why do we need permanent plots in the study of long-term vegetation dynamics? *J. Veg. Sci.* 7: 147-156.
- Bakker, J.P., Poschlod, P., Strykstra, R.J., Bekker, R.M. & Thompson, K. 1996. Seed banks and seed dispersal: Important topics in restoration ecology. *Acta Bot. Neerl.* 45: 461-490.
- Bal, D., H.M. Beije, M. Fellinger, R. Haveman, A.J.F.M. van Opstal & F.J. van Zadelhoff. 2001. *Handboek natuurdoeltypen*. Rapport EC-LNV 2001-20, 832 pp.
- Balmford, A., L. Bennun, B. ten Brink, D. et al. 2005. The Convention on Biological Diversity's 2010 Target. *Science* 307: 212-213.
- Baskin, C.C. & J.M. Baskin. 1998. *Seeds: Ecology, biogeography, and evolution of dormancy and germination*. Academic Press, San Diego.
- Baskin, J.M. & C.C. Baskin. 2004. A classification system for seed dormancy. *Seed Sci. Res.* 14: 1-16.
- Bazzaz, F.A., Ackerly, D.D. & Reekie, E.G. 2000. *Reproductive allocation in plants. Seeds: the ecology of regeneration in plant communities* (ed. M. Fenner), pp. 1-30. CABI Publishing, Wallingford.
- Beaufoy, D Baldock & J Clark (Eds.), 1994. *The nature of farming. Low intensity farming systems in nine European countries*. London, Joint Nature Conservation Committee.

- Bekker, R.M. & E.J. Lammerts 2002. Groene Stippen voor Rode Lijstsoorten: evaluatie van herstelmaatregelen. *De Levende Natuur* 103: 48-52.
- Bekker, R.M., Bakker, J.P., Grandin, U., Kalamees, R., Milberg, P., Poschlod, P., Thompson, K. & Willems, J.H. 1998b. Seed size, shape and vertical distribution in the soil: indicators of seed longevity. *Funct. Ecol.* 12: 834-842.
- Bekker, R.M., G.L. Verweij, R.E.N. Smit, R. Reine, J.P. Bakker & S. Schneider. 1997. Soil seed banks in European grasslands: does land use affect regeneration perspectives? *J. Appl. Ecol.* 34: 1293-1310.
- Bekker, R.M., Schaminée, J.H.J., Bakker, J.P. & Thompson, K. 1998. Seed bank characteristics of Dutch plant communities. *Acta Bot. Neerl.* 47: 15-26.
- Bell, G. 2000. The distribution of abundance in neutral communities. *Am. Nat.* 155: 606-617.
- Bell, G. 2001. Neutral macroecology. *Science* 293: 2413-2418.
- Bengtsson, J., Angelstam P., Elmqvist T., Emanuelsson U., Folke C., Ihse M., Moberg F. & Nystrom M 2003. Reserves, resilience and dynamic landscapes. *Ambio* 32: 389-396.
- Berendse, F. 2005. Impacts of global change on plant diversity and vice versa: Old and new challenges for vegetation scientists. *J. Veg. Sci.* 16: 613-616.
- Berendse, F., D. Chamberlain, D. Kleijn & H. Schekkerman. 2004. Declining biodiversity in agricultural landscapes and the effectiveness of agri-environment schemes. *Ambio* 33: 499-502.
- Berendse, F., Elberse W.T., Geerts, R.H.M.E. 1992. Competition and nitrogen loss from plants in grassland ecosystems. *Ecology* 73: 46-53.
- Bieleman, J. 1987. *Agrarian change in the Dutch province of Drenthe 1600-1910*. PhD-thesis University of Wageningen. [in Dutch with English summary].
- Bignal, E.M. & D.I. McCracken. 1996. Low-intensity farming systems in the conservation of the countryside. *J. Appl. Ecol.* 33: 413-424.
- Bijlsma, R.J., H. van Blitterswijk, A.P.P.M. Clercx & J.J. de Jong. 2002. Bospaden: een vertrouwd vangnet voor bosplanten. *Nederlands Bosbouw tijdschrift* 74: 10-15. [In Dutch]
- Bill, H.-Ch., Poschlod, P., Reich, M. & Plachter, H. 1999. Experiments and observations on seed dispersal by running water in an Alpine floodplain. *Bull. Geobot. Inst. ETH* 65: 13-28.
- Bissels, S., N. Hölzel, T.W. Donath & A. Otte. 2004. Evaluation of restoration success in alluvial grasslands under contrasting flooding regimes. *Biol. Conserv.* 118: 641-650.
- Blackshaw, R.E. & Rode, L.M. 1991. Effect of ensiling and rumen digestion by cattle on weed seed viability. *Weed Sci.* 39: 104-108.
- Blomqvist, M.M., P. Vos, P.G.L. Klinkhamer & W.J. Ter Keurs. 2003. Declining plant species richness of grassland ditch banks - a problem of colonisation or extinction? *Biol. Conserv.* 109: 391-406.
- Bobbink, R. 1991. Effects of nutrient enrichment in Dutch chalk grassland. *J. Appl. Ecol.* 28: 28-41.
- Bobbink, R., M. Hornung & J.G.M. Roelofs. 1998. The effect of air-borne nitrogen pollutant on species diversity in natural and semi-natural European vegetation. *J. Ecol.* 86: 717-738.
- Bodmer, R.E. 1990. Ungulate herbivores and the browser-grazer continuum. *Oikos* 57: 319-325.
- Boedeltje, G., Bakker, J.P., Bekker, R.M., Van Groenendael J.M. & Soesbergen, M. 2003. Plant dispersal in a lowland stream in relation to occurrence and three specific life-history traits of species in the species pool. *J. Ecol.* 91: 855-866.
- Boedeltje, G., J.P. Bakker, A. Ten Brinke, J.M. Van Groenendael & M. Soesbergen. 2004. Dispersal phenology of hydrochorous plants in relation to discharge, seed release time and buoyancy of seeds: the flood pulse concept supported. *J. Ecol.* 92: 786-796.
- Boedeltje, G., Ter Heerdt, G.N.J., Bakker, J.P. 2002. Applying the seedling-emergence method under waterlogged conditions to detect the seed bank of aquatic plants in submerged sediments. *Aquat. Bot.* 72: 121-128.
- Boedeltje, G., W.A. Ozinga & A. Prinzing. 2007. The trade-off between vegetative and generative reproduction across Angiosperms influences regional hydrochorous propagule pressure. *Global Ecol. Biogeogr.* (in press)
- Bokdam, J. & J.M. Gleichman. 2000. Effects of grazing by free-ranging cattle on vegetation dynamics in a continental north-west European heathland. *J. Appl. Ecol.* 37: 415-431.
- Bonn, S. & Poschlod, P. 1998. *Ausbreitungsbiologie der Pflanzen Mitteleuropas*. Quelle & Meyer Verlag, Wiesbaden. [in German].
- Bonn, S., Poschlod, P. & Tackenberg, O. 2000. Diasporus - a database for diaspore dispersal - concept and applications in case studies for risk applications in case studies for risk assessment. *Zeitschrift für Ökologie und Naturschutz* 9: 85-97.
- Booth, R.E. & J.P. Grime 2003. Effects of genetic impoverishment on plant community diversity. *J. Ecol.* 91: 721-730.
- Bossuyt, B., Hermys M., Deckers J. 1999. Migration of herbaceous plant species across ancient-recent forest ecotones in central Belgium. *J. Ecol.* 87: 628-638.
- Bossuyt, B., Honnay, O. & Hermys M. 2003. An island biogeographical view of the successional pathway in wet dune slacks. *J. Veg. Sci.* 14: 781-788.
- Bossuyt, B., O. Honnay & M. Hermys. 2004. Scale-dependent frequency distributions of plant species in dune slacks: Dispersal and niche limitation. *J. Veg. Sci.* 15: 323-330.
- Bouman, F., Boesewinkel, D., Bregman, R., Deventer, N. & Oostermeijer, J.G.B. 2000. *Verspreiding van zaden*. KNNV Uitgeverij, Utrecht. [In Dutch]

- Braakhekke, W.G. & D.A.P. Hooftman. 1999. The resource balance hypothesis of plant species diversity in grassland. *J. Veg. Sci.* 10: 187-200.
- Braun-Blanquet, J. 1932. *Plant sociology – The study of plant communities*. Authorized English translation of 'Pflanzensoziologie'. McGraw-Hill Book Comp., New York.
- Brokaw, N. & Busing, R.T. 2000. Niche versus chance and tree diversity in forest gaps. *Trends Ecol. Evol.* 15: 183-188.
- Brown, A.G. 2002. Learning from the past: palaeohydrology and palaeoecology. *Freshwat. Biol.* 47: 817-829.
- Brown, J.H. & A. Kodric-Brown. 1977. Turnover rates in insular biogeography: Effect of immigration on extinction. *Ecology* 58: 445-449.
- Brown, J.H. & B.A. Maurer. 1998. Macroecology: the division of food and space among species and continents. *Science* 243: 1145-1150.
- Brown, J.H. 1984. On the relationship between abundance and distribution of species. *Am. Nat.* 124: 255-279.
- Brown, J.H. 1999. Macroecology: progress and prospects. *Oikos* 87: 3-13.
- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. 2004. Towards a metabolic theory on ecology. *Ecology* 85: 1770-1789.
- Brown, V.K. 1992. Plant succession and life history strategy. *Trends Ecol. Evol.* 7: 143-144.
- Bruinderink, G.G., T. van Der Sluis, D. Lammertsma, P. Opdam & R. Pouwels 2003. Designing a coherent ecological network for large mammals in northwestern Europe. *Conserv. Biol.* 17: 549-557.
- Bruun, H.H. & B. Fritzboøger. 2002. The past impact of livestock husbandry on dispersal of plant seeds in the landscape of Denmark. *Ambio* 31: 425-431.
- Bullock, J.M. & Clarke, R.T. 2000. Long distance seed dispersal by wind: measuring and modelling the tail of the curve. *Oecologia* 124: 506-521.
- Bullock, J.M. & K.H. Hodder. 1997. Reintroductions: Challenges and lessons for basic ecology. *Trends Ecol. Evol.* 12: 68-69.
- Bullock, J.M., Clear Hill, B., Silvertown, J. & Sutton, M. 1995. Gap colonization as a source of grassland community change: effects of gap size and grazing on the rate and mode of colonization by different species. *Oikos* 72: 273-282.
- Bullock, J.M., I.L. Moy, R.F. Pywell, S.J. Coulson, A.M. Nolan & H. Caswell. 2002. Plant dispersal and colonization processed at local and landscape scales. In: J.M. Bullock, R.E. Kenward & R. Hails. *Dispersal Ecology*, pp. 279-302. Blackwell Science, Oxford.
- Bullock, S.H. & Primack, R.B. 1977. Comparative experimental study of seed dispersal on animals. *Ecology* 58: 681-686.
- Bunce, R.G.H., M. Pérez-Soba, R.H.G. Jongman et al. 2004. *Transhumance and biodiversity in european mountains, Report of the EU-FP5 project Transhumant*. IALE publication nr 1.
- Bunzel-Drüke, M., J. Drüke, L. Hauswirth & H. Vierhaus. 1999. Großtiere und Landschaft - Von der Praxis zur Theorie. *Natur- und Kulturlandschaft* 3: 210-229.
- Burke, M.J.W. & Grime, J.P. 1996. An experimental study of plant community invasability. *Ecology* 77: 776-790.
- Burny, J. 1999. Bijdrage tot de historische ecologie van de Limburgse Kempen (1910-1950). *Nat. Hist. Gen. Limburg* 42(1). [In Dutch]
- Burrows, F.M. 1975. Wind-born seed and fruit movement. *New Phytol.* 75: 405-418.
- Burt, A. 1989. Comparative methods using phylogenetically independent contrasts. *Oxf. Surv. Evol. Biol.* 6: 33-53.
- Cain, M.L., Damman, H. & Muir, A. 1998. Seed dispersal and the Holocene migration of woodland herbs. *Ecol. Monogr.* 68, 325-347.
- Cain, M.L., Milligan, B.G. & Strand, A.E. 2000. Long-distance seed dispersal in plant populations. *Am. J. Bot.* 87: 1217-1227.
- Campbell, J.E. & Gibson, D.J. 2001. The effect of seeds of exotic species transported via horse dung on vegetation along trail corridors. *Plant Ecol.* 157: 23-35.
- Cappers, R.T.J., R.M. Bekker & J.E.A. Jans, 2006. *Digital seed atlas of the Netherlands*. Groningen Archaeological Studies 4. Barkhuis Publishing, Eelde.
- Carey, P.D. 2001. Schemes are monitored and effective in the UK. *Nature* 414: 687.
- Carlquist, S. 1981. Chance dispersal. *Am. Sci.* 69: 509-516.
- Chang, E.R., Zozaya E.L., Kuijper D.P.J., Bakker J.P. 2005. Seed dispersal by small herbivores and tidal water: are they important filters in the assembly of salt-marsh communities? *Funct. Ecol.* 19: 665-673.
- Charlesworth, D. & B. Charlesworth 1987. Inbreeding Depression and its Evolutionary Consequences. *Ann. Rev. Ecol. Syst.* 18: 237-268.
- Chase, J.M. & M.A. Liebold. 2003. *Ecological niches: linking classical and contemporary approaches*. The University of Chicago Press, Chicago, Illinois.
- Chave, J. 2004. Neutral theory and community ecology. *Ecology Letters* 7: 241-253.
- Chave, J., Muller-Landau, H.C. & Levin, S.A. 2002. Comparing classical community models: theoretical consequences for patterns of diversity. *Am. Nat.* 159: 1-23.
- Cheffings, C.M. & Farrell, L., Dines, T.D. et al. 2005. The Vascular Plant Red Data List for Great Britain. *Species Status* 7: 1-116.
- Chesson, P. & N. Huntly. 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *Am. Nat.* 150: 519-553.

- Chesson, P.L. & Warner R.R. (1981): Environmental variability promotes coexistence in lottery competitive systems. *Am. Nat.* 117: 923-943.
- Christensen, J.H. & O.B. Christensen. 2003. Severe summertime flooding in Europe. *Nature* 421: 805.
- Chytrý, M. 2001. Phytosociological databases give biased estimates of species richness. *J. Veg. Sci.* 12: 439-444.
- Clark, J.S. 1998. Why trees migrate so fast: Confronting theory with dispersal biology and the paleorecord. *Am. Nat.*, 152, 204-224.
- Clark, J.S., Fastie, C., Hurr, G., Jackson, S.T. et al. 1998. Reid's paradox of rapid plant migration. *BioScience*, 48, 13-24.
- Clark, M. Silman, J.S., Kern, R., Macklin, E. & HilleRisLambers, J. 1999. Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology* 80: 1475-1494.
- Clauss, M., Lechner-Doll, M. & Streich, W.J. 2003. Ruminant diversification as an adaptation to the physicochemical characteristics of forage. A reevaluation of an old debate and a new hypothesis. *Oikos* 102: 253-262.
- Clements, F.E. 1928. *Plant succession and indicators*. - H.W. Wilson, New York.
- Coley, P.D., Bryant, J.P. & Chapin III, F.S. 1985. Resource availability and plant anti-herbivore defence. *Science* 230: 895-899.
- Collins, S.L. & Uno, G.E. 1985. Seed predation, seed dispersal, and disturbance in grasslands: a comment. *Am. Nat.* 125: 866-872.
- Collins, S.L., S.M. Glenn & D.W. Roberts. 1993. The hierarchical continuum concept. *J. Veg. Sci.* 4: 149-156.
- Combroux, I., Bornette G., Willby, N.J. & Amoros, C. 2001. Regeneration strategies of aquatic plants in disturbed habitats: the role of the propagule bank. *Archiv Hydrobiologia* 152: 215-235.
- Condit, R., Ashton PS, Baker P, Bunyavejchewin S, Gunatilleke S, Gunatilleke N, Hubbell SP et al. 2000. Spatial patterns in the distribution of tropical tree species. *Science* 288: 1414-1418.
- Condit, R. et al. 2006. The importance of demographic niches to tree diversity. *Science* 313: 98-101.
- Connell, J.H. 1978 Diversity in tropical rain forests and coral reefs. *Science* 199: 1302-1310.
- Connor, E.F. & D. Simberloff. 1979. The assembly of species communities: chance or competition? *Ecology* 61: 1132-1140.
- Cook, R.E. 1983. Clonal plant populations. *Am. Sci.* 71: 244-254.
- Cook, W.M., J. Yao, B.L. Foster, R.D. Holt & L.B. Patrick. 2005. Secondary succession in an experimentally fragmented landscape: Community patterns across space and time. *Ecology* 86: 1267-1279.
- Coomes, D.A. & Grubb P.J. 2003. Colonization, tolerance, competition and seed-size variation within functional groups. *Trends Ecol. Evol.* 18: 283-291.
- Cornelissen, J.H.C., Lavorel, S., Garnier, E., Diaz, S. et al. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Aust. J. Bot.* 51: 335-380.
- Cornell, H.V. & Karlson R.H. 1997. Local and regional processes as controls of species richness. In: Tilman D. & Kareiva P. (eds.), *Spatial ecology. The role of space in population dynamics and interspecific interactions*. Princeton Univ. Press, New Jersey. Pp. 250-268.
- Cornell, H.V. 1993. Unsaturated patterns in species assemblages: the role of regional processes in setting local species richness. In: Ricklefs R.E. & Schluter D. (eds.), *Species diversity in ecological communities*. pp. 243-252.
- Cornell, H.V. 1999. Unsaturation and regional influences on species richness in ecological communities: A review of evidence. *EcoScience* 6: 303-315.
- Cornwell, W.K., D.W. Schilck, & D.D. Ackerly. 2006. A trait-based test for habitat filtering: convex hull volume. *Ecology* 87: 1465-1471.
- Cosyns, E. & M. Hoffmann. 2005. Horse dung germinable seed content in relation to plant species abundance, diet composition and seed characteristics. *Basic Appl. Ecol.* 6: 11-24.
- Cosyns, E., A. Delporte, L. Lens & M. Hoffmann. 2005. Germination success of temperate grassland species after passage through ungulate and rabbit guts. *J. Ecol.* 93: 353-361.
- Cosyns, E., B. Bossuyt, M. Hoffmann, b, H. Vervaeke, L. Lens 2005. Seedling establishment after endozoochory in disturbed and undisturbed grasslands. *Basic Appl. Ecol.* 7: 360-369.
- Coulson, S., J.M. Bullock, M.J. Stevenson & R.F. Pywell. 2001. Colonization of grassland by sown species: dispersal versus microsite limitation in responses to management. *J. Appl. Ecol.* 38: 204-216.
- Council of Europe, 2000. Guidelines for the development of the Pan European Ecological Network for Central and Eastern Europe. *Nature and Environment* 107. Council of Europe Publishing, Strasbourg.
- Cousins, S.A.O., Lavorel S. & Davies I. 2003. Modelling the effects of landscape pattern and grazing regimes on the persistence of plant species with high conservation value in grasslands in south-eastern Sweden. *Landsc. Ecol.* 18: 315-332.
- Cousins, S.A.O., Ohlson, H. & Eriksson, O. 2007. Effects of historical and present fragmentation on plant species diversity in semi-natural grasslands in Swedish rural landscapes. *Landsc. Ecol.* 22: 723-730.
- Couvreux, M., B. Christiaen, K. Verheyen & M. Hermy. 2004. Herbivores as mobile links within and between isolated nature reserves through adhesive seed dispersal. *Applied Vegetation Science* 7: 229-236.
- Couvreux, M., B. VandenBerghe, K. Verheyen & M. Hermy. 2005. Complementarity of epi- and endozoochory of plant seeds by free ranging donkeys. *Ecography* 28: 37-48.
- Couvreux, M., B. VandenBerghe, K. Verheyen & M. Hermy. 2005. Experimental assessment of plant seed retention times in fur of cattle and horse. *Flora* 200: 136-147.

- Couvreur, M., Vandenbergh, B., Verheyen, K. & Hermy, M. 2004. An experimental assessment of seed adhesivity on animal furs. *Seed Science Research* 14: 147–159.
- Cramp, S., Simmons, K.E.L. & Perrins, C.M. (eds.) 1977–1994. *Handbook of the birds of Europe, North Africa and the Middle East*. 1–9. Oxford University Press.
- Crawley, M.J. 1990. The population biology of plants. *Phil. Trans. R. Soc. Lond. Biol. Sci.* 330: 125–140.
- Dai, X. 2000. Impact of cattle dung deposition on the distribution pattern of plant species in an alvar limestone grassland. *J. Veg. Sci.* 11: 715–724.
- Dale, V.H. 1989. Wind dispersed seeds and plant recovery on Mount St. Helens debris avalanche. *Can. J. Bot.* 67: 1434–1441.
- Dale, V.H., A.E. Lugo, J.A. MacMahon & S.T.A. Pickett. 1998. Ecosystem management in the context of large, infrequent disturbances. *Ecosystems* 1: 546–557.
- Dalling, J.W. & S.P. Hubbell. 2002. Seed size, growth rate and gap microsite conditions as determinants of recruitment success for pioneer species. *J. Ecol.* 90: 557–568.
- Dalling, J.W., Hubbell S.P., Silveira K. 1998. Seed dispersal, seedling establishment and gap partitioning among tropical pioneer trees. *J. Ecol.* 86: 674–689.
- Danvind, M. & C. Nilsson. 1997. Seed floating ability and distribution of alpine plants along a northern Swedish river. *J. Veg. Sci.* 8: 271–276.
- Davidson, D.W. 1993 The effects of herbivory and granivory on terrestrial plant succession. *Oikos* 68: 23–35.
- Davis, M.A., Grime, J.P. & Thompson, K. 2000. Fluctuating resources in plant communities: a general theory of invasibility. *J. Ecol.* 88: 528–534.
- Davis, M.A., K. Thompson & Grime, J.P. 2005. Invasibility: the local mechanism driving community assembly and species diversity. *Ecography* 28: 696–704.
- De Deyn, G.B. & W.H. Van der Putten. 2005. Linking aboveground and belowground diversity. *Trends Ecol. Evol.* 20: 625–633.
- De Vries, V. 1939. Verspreiding van plantenzaden door vogels. *De Levende Natuur* 43: 245–350; 43: 210–215; 43: 279–284; 308–312 [in Dutch].
- Debusche, M. & Isenmann, P. 1994. Bird-dispersed seed rain and seedling establishment in patchy Mediterranean vegetation. *Oikos* 69: 414–426.
- Delbaere, B.C.W. 2002. European policy review. *J. Nat. Conserv.* 10: 125–126.
- Delbaere, B.C.W. 2006. European policy review - Assessing policy impacts on biodiversity. *J. Nat. Conserv.* 14, 129–130.
- Demment, M.W. & Van Soest, P.J. 1985. A nutritional explanation for body-size patterns of ruminant and non-ruminant herbivores. *Am. Nat.* 125: 641–672.
- Diamond, J.M. (1975). Assembly of species communities. In: *Ecology and Evolution of Communities*. (eds. M.L. Cody & J.M. Diamond), 342–444. Harvard University Press, Cambridge.
- Diamond, J.M. 1991. World of living death. *Nat. Hist.* 9: 30.
- Díaz, S., Fargione J, Chapin FS, et al. 2006. Biodiversity loss threatens human well-being. *PLOS Biology* 4: 1300–1305.
- Díaz, S. & Cabido, M. 2001. Vive la différence: plant functional diversity matters to ecosystem processes. *Trends Ecol. Evol.* 16: 646–655.
- Díaz, S., Cabido, M. & Casanoves, F. 1999. Functional implications of trait-environment linkages in plant communities. In: E. Weiher & P.A. Keddy, *Ecological assembly rules. Perspectives, advances, retreats*. Cambridge Univ. Press. Pp. 338–362.
- Díaz, S., Cabido, M. & Casanoves, F. 1998. Plant functional traits and environmental filters at a regional scale. *J. Veg. Sci.* 9: 113–122.
- Díaz, S., Hodgson, J.G., Thompson, K. et al. 2004. The plant traits that drive ecosystems: Evidence from three continents. *J. Veg. Sci.* 15: 295–304.
- Diekmann, M. 2003. Species indicator values as an important tool in applied plant ecology - a review. *Basic Appl. Ecol.* 4: 493–506.
- Dobson, A.P., A.D. Bradshaw & A.J.M. Baker. 1997. Hopes for the future: restoration ecology and conservation biology. *Science* 277: 515–522.
- Dodd, M.E., J. Silvertown, K. McConway, J. Potts & M. Crawley. 1995. Community stability: a 60 year record of trends and outbreaks in the occurrence of species in the Park Grass experiment. *J. Ecol.* 83: 277–285.
- Dolédec, S., D. Chessel, C. J. F. Ter Braak, & S. Champely. 1996. Matching species traits to environmental variables: a new three-table ordination method. *Environmental and Ecological Statistics* 3:143–166.
- Dolek, M. & A. Geyer. 2002. Conserving biodiversity on calcareous grasslands in the Franconian Jura by grazing: a comprehensive approach. *Biol. Cons.* 104: 351–360.
- Dorland, E., L.J.L. van den Berg, E. Brouwer, J.G.M. Roelofs & R. Bobbink. 2005. Catchment liming to restore degraded, acidified heathlands and moorland pools. *Restor. Ecol.* 13: 302–311.
- Dupré, C. 2000. How to determine a regional species pool: a study in two Swedish regions. *Oikos* 89: 128–136.
- Dynesius, M. & C. Nilsson. 1994. Fragmentation and flow regulation of river systems in the northern third of the world. *Science* 266: 753–762.
- Eckert, C.G. 2002. The loss of sex in clonal plants. *Evol. Ecol.* 15: 501–520.
- Ecklund, O. 1927. Versuche über das Kiemungs- und Schwimmvermögen einiger Samen und Früchte im Ostseewasser. *Mém. Soc. Fauna et Flora Fennica* 10: 2–13.

- Edelman, C.H., 1934. Harm Tiesing over landbouw en volksleven in Drenthe. Van Gorcum & Comp. bv, Assen.
- Ehrlén, J. & Eriksson O. 2000. Dispersal limitation and patch occupancy in forest herbs. *Ecology* 81: 1667-1674.
- Ehrlén, J. & Lehtilä, K. 2002. How perennial are perennial plants? *Oikos* 98: 308-322.
- Ehrlén, J. & Van Groenendael J.M. 1998. The trade-off between dispersability and longevity - an important aspect of plant species diversity. *Appl. Veg. Sci.* 1: 29-36.
- Eikelboom, H. 1941-1942. Over de endozoische verspreiding van zaad door eenden. I en II *Limosa* 14: 108-114; 15: 13-19. [in Dutch].
- Ejrnæs, R., H.H. Bruun & B.J. Graae 2006. Community assembly in experimental grasslands: suitable environment or timely arrival? *Ecology* 87: 1225-1233.
- Elerie, J.N.H., 1998. Weerbarstig land. *Een historisch-ecologische landschapsstudie van Koekange en de Reest*. PhD-thesis Wageningen University. [in Dutch with English summary].
- Ellenberg, H. 1988. *Vegetation Ecology of Central Europe*. 4th edition. Cambridge Univ. Press., Cambridge, UK.
- Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W. & Paulißen, D. 1992. Zeigerwerte von Pflanzen in Mitteleuropa, 2nd edn. *Scripta Geobot.* 18: 1-258. Goltze, Göttingen. [3rd edn. in 2001; In German]
- Ellstrand, N.C. & D.R. Elam. 1993. Population genetic consequences of small population-size - implications for plant conservation. *Ann. Rev. Ecol. Syst.* 24: 217-242.
- Enquist, B.J., West, G.B., Charnov, E.L. & Brown, J.H. 1999. Allometric scaling of productivity and life-history variation in vascular plants. *Nature* 401: 907-911.
- Eriksson, O. & A. Jakobsson. 1998. Abundance, distribution and life histories of grassland plants: a comparative study of 81 species. *J. Ecol.* 86: 922-933.
- Eriksson, O. & H. Froberg. 1996. "Windows of opportunity" for recruitment in long-lived clonal plants: experimental studies of seedling establishment in *Vaccinium* shrubs. *Can. J. Bot.* 74: 1369-1374.
- Eriksson, O. & J. Ehrlén. 1992. Seed and microsite limitation of recruitment in plant populations. *Oecologia* 91: 360-364.
- Eriksson, O. 1993 The species-pool hypothesis and plant community diversity. *Oikos* 68: 371-374.
- Eriksson, O. 1996. Regional dynamics of plants: a review of evidence for remnant, source-sink and metapopulations. *Oikos* 77: 248-258.
- Eriksson, O. 2000. Seed dispersal and colonization ability of plants - assessment and implications for conservation. *Folia Geobot.* 35: 115-123.
- Eriksson, O. 2002. Ontogenetic niche shifts and their implications for recruitment in three clonal *Vaccinium* shrubs: *Vaccinium myrtillus*, *Vaccinium vitis-idaea*, and *Vaccinium oxycoccus*. *Can. J. Bot.* 80: 635-641.
- Eriksson, O., S.A.O. Cousins & R. Lindborg. 2005. Land use history and the build-up and decline of species richness in Scandinavian semi-natural grasslands. In: J.A. Milne (Ed.): *Pastoral systems in marginal environments*. Wageningen Ac. Publ.
- Etienne, R.S. & D. Alonso. 2005. A dispersal-limited sampling theory for species and alleles. *Ecol. Lett.* 8: 1147-1156.
- Etienne, R.S. & H. Olff. 2004. A novel genealogical approach to neutral biodiversity theory. *Ecol. Lett.* 7: 170-175.
- Etienne, R.S. & H. Olff. 2005. Confronting different models of community structure to species-abundance data: a Bayesian model comparison. *Ecol. Lett.* 8: 593-504.
- European Commission, 2003. Europe's environment: the third assessment. *Environmental Assessment Report No 10*, Luxembourg: Office for Official Publications of the European Communities, 341pp.
- European Environment Agency, 2005. *The European environment - State and outlook*. European Environment Agency, Copenhagen.
- European Union, 1992. *Habitats Directive*. Council Directive 92/43/ECC, Brussels.
- Evard, M. 2005. *Water meadows*. Antony Rowe Ltd. Eastborne, East Sussex.
- Ewald, J. 2002. A probabilistic approach to estimating species pools from large compositional matrices. *J. Veg. Sci.* 13: 191-198.
- Ewald, J. 2003. A critique for phytosociology. *J. Veg. Sci.* 14: 291-296.
- Feekes, W. 1936. *De ontwikkelingen van de natuurlijke vegetatie in de Wieringermeerpolder, de eerste groote droogmakerij van de Zuiderzee*. PhD Thesis, University of Wageningen. [in Dutch].
- Fenner, M. & Thompson, K. 2005. *The ecology of seeds*. Cambridge Univ. Press, Cambridge.
- Figuerola, J. & Green A.J. 2002. Dispersal of aquatic organisms by waterbirds: a review of past research and priorities for future studies. *Freshwater Biology* 47: 483-494.
- Fischer, S., Poschold, P. & Beinlich, B. 1996. Experimental studies on the dispersal of plants and animals by sheep in calcareous grasslands. *J. Appl. Ecol.* 33: 1206-1222.
- Fitter, A.H. 2005. Darkness visible: reflections on underground ecology. *J. Ecol.* 93: 231-243.
- Foster, B.L. & Dickson, T.L. 2004. Grassland diversity and productivity: the interplay of resource availability and propagule pools. *Ecology* 85: 1541-1547.
- Foster, B.L. & Tilman, D. 2000. Dynamic and static views of succession: Testing the descriptive power of the chronosequence approach. *Plant Ecol.* 146: 1-10.
- Foster, B.L. & Tilman, D. 2003. Seed limitation and the regulation of community structure in oak savanna grassland. *J. Ecol.* 91: 999-1007.
- Foster, B.L., T.L. Dickson, C.A. Murphy, I.S. Karel & V.H. Smith. 2004. Propagule pools mediate community assembly and diversity-ecosystem regulation along a grassland productivity gradient. *J. Ecol.* 92: 435-449.

- Fowler, N.L. 1988. What is a safe site? Neighbor, litter, germination date, and patch effects. *Ecology* 69: 947-961.
- Freckleton, R.P. & Watkinson, A.R. (2002) Large-scale spatial dynamics of plants: metapopulations, regional ensembles and patchy populations. *J. Ecol.* 90: 419-434.
- Freeland, W.J. & D.H. Janzen. 1974. Strategies in herbivory by mammals: The role of plant secondary compounds. *Am. Nat.* 108: 269-289.
- Funes, G., Basconcelo S., Diaz S., Cabido M. 1999. Seed size and shape predict seed persistence in the soil bank in grasslands of central Argentina. *Seed Sci. Res.* 9: 341-345.
- García, D. & Zamora, R. 2003. Persistence, multiple demographic strategies and conservation in long-lived Mediterranean plants. *J. Veg. Sci.* 14: 921-926.
- Gardener, C.J., McIvor, J.G. & Jansen, A. 1993. Passage of legume and grass seeds through the digestive tract of cattle and their survival in faeces. *J. Appl. Ecol.* 30: 63-74.
- Gardener, C.J., McIvor, J.G. & Jansen, A. 1993. Survival of seeds of tropical grassland species subjected to bovine digestion. *J. Appl. Ecol.* 30: 75-85.
- Gauch, H.G. 1982. Multivariate analysis in community ecology. Cambridge Univ. Press, Cambridge.
- Geertsema, W. 2002. *Plant survival in dynamic habitat networks in agricultural landscapes*. PhD-thesis University of Wageningen.
- Geertsema, W. 2005. Spatial dynamics of plant species in an agricultural landscape in the Netherlands. *Plant Ecol.* 178: 237-247.
- Genard, M. & Lescourret, F. 1985. Le sanglier (*Sus scrofa scrofa* L.) et les diaspores dans le sud de France. *Rev. Ecol.* 40: 343-353. [In French]
- Ghassali, F., Osman, A.E., Cocks, P.S. 1998. Rehabilitation of degraded grasslands in north Syria: The use of Awassi sheep to disperse the seeds of annual pasture legumes. *Exp. Agric.* 34: 391-405.
- Gijsbers, W.M. 1999. *Kapitale ossen. De internationale handel in slachtvee in Noordwest-Europa (1300-1750)*. PhD thesis University of Amsterdam. [In Dutch]
- Gijsbers, W.M. 2002. Een enkele reis over de ossenwegen. *Historisch-Geografisch Tijdschrift* 20: 62-66. [A one-way trip over the ox routes; In Dutch with English summary]
- Gilpin, M.E. & Soulé, M.E. 1986. Minimum viable populations: processes of species extinction. In: M.E. Soulé (ed.): *Conservation biology; The Science of Scarcity and Diversity* (ed. M. E. Soulé) 19-34 (1986).
- Gitay, H. & Noble, I.R. 1997. What are functional types and how should we seek them? In: T.M. Smith, Shugart, H.H. & Woodward, I.H. (eds.) *GCTE workshop on plant functional types*, pp. 3-19. Cambridge Univ. Press, UK.
- Gleason, H.A. 1926. The individualistic concept of the plant association. - *Bulletin of the Torrey Botanical Club* 53: 1-20.
- Godwin, F. & S. Toulson. 1977. *The drovers' roads of Wales*. London, Wildwood House.
- Gorb, E. & Gorb, S. 2002. Contact separation force of the fruit burrs in four plant species adopted to dispersal by mechanical interlocking. *Plant Physiol. Biochem.* 40: 373-381.
- Gotelli, N.J. 2000. Null model analysis of species co-occurrence patterns. *Ecology* 81: 2606-2621.
- Gotelli, N.J. 2001. Research frontiers in null model analysis. *Global Ecology & Biogeography* 10: 337-343.
- Gottschalk, M.K.E. 1977. Storm surges and river floods in the Netherlands. *Social Geographical Studies* 14.
- Graae, B.J. 2002. The role of epizoochorous seed dispersal of forest plant species in a fragmented landscape. *Seed Sci. Res.* 12: 113-121.
- Grace, J. 1977. *Plant responses to wind*. Academic Press, London.
- Grace, J.B. 1993. The adaptive significans of clonal reproduction in angiosperms: an aquatic perspective. *Aquat. Bot.* 44: 159-180.
- Grace, J.B. 1999. The factors controlling species density in herbaceous plant communities: an assessment. *Perspect. Plant Ecol. Evol. Syst.* 2: 1-28.
- Grashof-Bokdam C.J. & F. van Langevelde, 2005. Green veining: landscape determinants of biodiversity in European agricultural landscapes. *Landsc. Ecol.* 20: 417-439.
- Grashof-Bokdam, C.J. & W. Geertsema. 1998. The effect of isolation and history on colonization patterns of plant species in secondary woodland. *J. Biogeogr.* 25: 837-846.
- Grashof-Bokdam, C.J. 1997. Colonization of forest plants: the role of fragmentation. Thesis Leiden University.
- Greene, D.F. & Johnson, E.A. 1989. A model of wind dispersal of winged and plumed seeds. *Ecology* 70: 339-347.
- Greene, D.F. & Johnson, E.A. 1993. Seed mass and dispersal capacity in wind- dispersed diaspores. *Oikos* 67: 69-74.
- Greene, D.F. & Johnson, E.A. 1996. Wind dispersal of seeds from a forest into a clearing. *Ecology* 77: 595-609.
- Grime, J.P. & Hunt, R. 1975. Relative growth-rate: its range and adaptive significance in a local flora. *J. Ecol.* 63: 393-422.
- Grime, J.P. & Jeffery, D.W. 1965. Seedling establishment in a vertical gradient of sunlight. *J. Ecol.* 53: 621-642.
- Grime, J.P. & S.H. Hillier. 1992. The contribution of seedling regeneration to the structure and dynamics of plant communities and larger units of landscape. In: M. Fenner (ed.): *Seeds - The ecology of regeneration in plant communities*. CAB International. pp. 349-365.
- Grime, J.P. 1973. Competitive exclusion in herbaceous vegetation. *Nature* 242: 344-347.
- Grime, J.P. 1974. Vegetation classification by reference to strategies. *Nature* 250: 26-31.

- Grime, J.P. 1977. Evidence for existence of 3 primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.* 111: 1169-1194.
- Grime, J.P. 1986. The circumstances and characteristics of spoil colonization within a local flora. *Phil. Transactions of the Royal Society London B* 314: 637-654.
- Grime, J.P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J. Ecol.* 86: 902-910.
- Grime, J.P. 2001. *Plant strategies, vegetation processes, and ecosystem properties*. Second edition. John Wiley & Sons, Ltd.
- Grime, J.P. 2002. Declining plant diversity: empty niches or functional shifts? *J. Veg. Sci.* 13: 457-460.
- Grime, J.P. 2006. Trait convergence and trait divergence in herbaceous plant communities: Mechanisms and consequences. *J. Veg. Sci.* 17: 255-260.
- Grime, J.P., G. Mason, A.V. Curtis, J. et al. 1981. A comparative study of germination characteristics in a local flora. *J. Ecol.* 69: 1017-1059.
- Grime, J.P., Mackey, J.M., Miller, S.H. & Read, D.J. 1987. Floristic diversity in a model system using experimental microcosm. *Nature* 328: 420-422.
- Grime, J.P., Thompson, K., Hunt, R. et al. 1997. Integrated screening validates primary axis of specialisation in plants. *Oikos* 79: 259-281.
- Groot Bruinderink, G., T. van der Sluis, D. Lammertsma, P. Opdam & R. Pouwels. 2003. Designing a coherent ecological network for large mammals in Northwestern Europe. *Cons. Biol.* 17: 549-557.
- Grootjans, A.P., Fresco L.F.M., De Leeuw C.C. & Schipper P.C. 1996. Degeneration of species-rich *Calthion palustris* hay meadows; some considerations on the community concept. *J. Veg. Sci.* 7: 185-194.
- Grootjans, A.P., J.P. Bakker, A.J.M. Jansen & R.H. Kemmers. 2002. Restoration of brook valley meadows in the Netherlands. *Hydrobiologica* 478: 149-170.
- Grubb, P.J. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biol. Rev.* 52: 107-145.
- Grubb, P.J. 1987. Some generalizing ideas about colonization and succession in green plants and fungi. In: A.J. Gay, M.J. Crawley & P.J. Edwards (eds.): *Colonization, succession and stability*, pp. 81-102. Blackwell, Oxford.
- Grubb, P.J., D. Kelly & J. Mitchley. 1982. The control of relative abundance in communities of herbaceous plants. In: E.I. Newman (ed.): *The plant community as a working mechanism*, pp 77-97. Blackwell Scientific Publications, Oxford, UK.
- Guppy, H.B. 1906. *Observations of a Naturalist in the Pacific between 1896 and 1899*. Vol. 2. Plant dispersal. Macmillan & co., London.
- Hamilton, M.A., Murray B.R., Cadotte M.W. et al. 2005. Life-history correlates of plant invasiveness at regional and continental scales. *Ecol. Lett.* 8: 1066-1074.
- Hanski, I. & Gaggiotti O.E. 2004. *Ecology, genetics, and evolution of metapopulations*. Elsevier Ac. Press, Amsterdam.
- Hanski, I. & Ovaskainen, O. 2002. Extinction debt at extinction threshold. *Cons. Biol.* 16: 666-673.
- Hanski, I. 1982. Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos* 38: 210-221.
- Hanski, I. 1998. Metapopulation dynamics. *Nature* 396: 41-49.
- Hanski, I. 1999. Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. *Oikos* 87: 209-219.
- Hanski, I. 2000. Extinction debt and species credit in boreal forests: modelling the consequences of different approaches to biodiversity conservation. *Annales Zoologici Fennici* 37: 271-280.
- Hanski, I., A. Moilanen & M. Gyllenberg. 1996. Minimal viable metapopulation size. *Am. Nat.* 147: 527-541.
- Harper, J.L., Lovell, P.H. & Moore, K. 1970. The shapes and sizes of seeds. *Ann. Rev. Ecol. Syst.* 1: 327-356.
- Harpole, W.S. & D. Tilman. 2006. Non-neutral patterns of species abundance in grassland communities. *Ecol. Lett.* 9: 15-23.
- Harpole, W.S. & D. Tilman. 2007. Grassland species loss resulting from reduced niche dimension. *Nature* 446: 791-793.
- Harrison, S., J. Maron & G. Huxel. 2000. Regional turnover and fluctuation in populations of five plants confined to serpentine seeps. *Cons. Biol.* 14: 769-779.
- Harte, J. 2004. The value of null theories in ecology. *Ecology* 85: 1792-1794.
- Hartley, S. & W.E. Kunin. 2003. Scale dependency of rarity, extinction risk, and conservation priority. *Conserv. Biol.* 17: 1559-1570.
- Harvey, P.H. & Pagel, M.D. 1991. *The Comparative Method in Evolutionary Biology*. Oxford University Press, Oxford.
- Hassan, R., R. Scholes & N. Ash. 2005. *Ecosystems and human well-being: current state and trends – Findings of the Condition and Trends Working Group*. Millennium Ecosystem Assessment, Island press.
- Hayward, I.M. & Druce, G.C. 1919. *The adventive flora of Tweedside*. Arbroath, T.Buncle & Co.
- Heinken, T. & Raudnitschka, D. 2002. Do wild ungulates contribute to the dispersal of vascular plants in Central European forests by epizoochory? A case study in NE Germany. *Forstwissenschaftliches Centralblatt* 121: 179-194.
- Heinken, T. Haspach, H. & Schaumann, F. 2002. Dispersal of vascular plants by four species of wild mammals in a deciduous forest in NE Germany. *Phytocoenologia* 32: 627-643.
- Heintze, A. 1932. *Handbuch der Verbreitungsökologie der Pflanzen*. Selbstverlag, 266. Stockholm. [In German].

- Helm, A., Hanski, I. & Pärtel, M. 2006. Slow response of plant species richness to habitat loss and fragmentation. *Ecol. Lett.* 9: 72-77.
- Hennekens, S.M. & Schaminée, J.H.J. 2001. TURBOVEG, Comprehensive data base management system for vegetation data. - *J. Veg. Sci.* 12: 589-591.
- Hensen, I. & Müller, C. 1997. Experimental and structural investigations of anemochorous dispersal. *Plant Ecol.* 133: 169-180.
- Herben, T. & Hara T. 2003. Spatial pattern formation in plant communities. In: Sekimura T., Noji S., Ueno N. & Maini P.K. (eds.), *Morphogenesis and Pattern Formation in Biological Systems - Experiments and Models*. Springer Verlag, pp. 223-235.
- Herben, T. 2000. Correlation between richness per unit area and the species pool cannot be used to demonstrate the species pool effect. *J. Veg. Sci.* 11: 123-126.
- Herben, T., F. Krahulec, V. Hadincová, S. Pechácková & M. Kovárová. 1997. Fine-scale spatio-temporal patterns in a mountain grassland: do species replace each other in a regular fashion? *J. Veg. Sci.* 8: 217-224.
- Hermý, M., O. Honnay, L. Firbank, C. Grashof-Bokdam & J. Lawesson. 1999. An ecological comparison between ancient and other forest plant species in Europe, and the implications for forest conservation. *Biol. Conserv.* 91: 9-22.
- Herrera, C.M. 1987. Vertebrate-dispersed plants of the Iberian Peninsula - A study of fruit characteristics. *Ecol. Monogr.* 57: 305-331.
- Herrera, C.M. 1989. Frugivory and seed dispersal by carnivorous mammals, and associated fruit characteristics, in undisturbed Mediterranean habitats. *Oikos* 55: 250-262.
- Herrera, C.M. 1995. Plant-vertebrate seed dispersal systems in the mediterranean, Ecological, evolutionary, and historical determinants. *Annu. Rev. Ecol. Syst.* 26: 705-727.
- Higgins, S.I. & D.M. Richardson. 1999. Predicting plant migration rates in a changing world: The role of long distance dispersal. *Am. Nat.* 153: 464-475.
- Higgins, S.I., Nathan, R. & Cain, M.L. 2003. Are long-distance dispersal events in plants usually caused by non-standard means of dispersal? *Ecology* 84: 1945-1956.
- Higgins, S.I., Richardson, D.M. & Cowling, R.M. 1996. Modeling invasive plant spread: The role of plant-environment interactions and model structure. *Ecology* 77: 2043-2054.
- Hill, M.O. & P.D. Carey. 1997. Prediction of yield in the Rothamsted Park Grass Experiment by Ellenberg indicator values. *J. Veg. Sci.* 8: 579-586.
- Hill, M.O. & Gauch, H.G. 1980. Detrended correspondence analysis, an improved ordination technique. *Vegetatio* 42: 47-58.
- Hill, M.O., Mountford, J.O., Roy, D.B. & Bunce, R.G.H. 1999. *Ellenberg's Indicator Values for British Plants*. Ecolfact Vol. 2, Technical Annex. Institute for Terrestrial Ecology, Transport and Regions (NERC), Huntingdon.
- Hillegers, H.P.M. 1985. Exozoochoor transport van diasporen door Mergellandschapen. *Natuurhistorisch Maandblad* 74: 54-56. [in Dutch].
- Hillegers, H.P.M. 1993. *Heerdgang in Zuidelijk Limburg: een vorm van extensieve beweiding in verleden, heden en toekomst*. PhD thesis, Maastricht. [In Dutch]
- Hobbs, N.T., S. Twombly & D. Schimel. 2006. Deepening ecological insights using contemporary statistics. *Ecol. Appl.* 16: 3-4.
- Hobbs, R.J. & Norton, D.A. 1996. Towards a conceptual framework for restoration ecology. *Rest. Ecol.* 4: 93-110.
- Hobbs, R.J. et al. 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecol. Biogeogr.* 15: 1-7.
- Hodder, K.H. & J.M. Bullock. 1997. Translocations of native species in the UK: Implications for biodiversity. *J. Appl. Ecol.* 34: 547-565.
- Hodgson, J.G. & J.P. Grime. 1990. The role of dispersal mechanisms, regenerative strategies and seed banks in the vegetation dynamics of the British landscape. In: R.G.H. Bunce & D.C. Howard (eds.): *Species dispersal in agricultural habitats*. London: Belhaven Press, 65-82.
- Hodgson, J.G., G. Montserrat-Martí, B. Cerabolini, R.M. et al. 2005. A functional method for classifying European grasslands for use in joint ecological and economic studies. *Basic Appl. Ecol.* 6: 119-131.
- Hodgson, J.G., Grime, J.P., Hunt, R. & Thompson, K. 1995. *The electronic comparative plant Ecology*. Chapman & Hall, London.
- Hodgson, J.G., Wilson, P.J., Hunt, R., Grime, J.P. & Thompson, K. 1999. Allocating C-S-R plant functional types: a soft approach to a hard problem. *Oikos* 85: 282-294.
- Hodkinson, D.J. & Thompson, K. 1997. Plant dispersal: The role of man. *J. Appl. Ecol.* 34: 1484-1496.
- Hodkinson, D.J., A.P. Askew, K. Thompson, J.G. Hodgson, J.P. Bakker & R.M. Bekker 1998. Ecological correlates of seed size in the British flora. *Funct. Ecol.* 12: 762-766.
- Hofmann, R.R. 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comprehensive view of their digestive system. *Oecologia* 78: 443-457.
- Hole, D.G., A.J. Perkins, J.D. Wilson, I.H. et al. 2005. Does organic farming benefit biodiversity? *Biol. Conserv.* 122: 113-130.
- Holyoak, M. & M. Loreau. 2006. Reconciling empirical ecology with neutral community models. *Ecology* 87: 1370-1377.
- Holyoak, M., M. Loreau & D. Strong. 2006. Neutral community ecology. *Ecology* 87: 1368-1369.

- Holyoak, M., M.A. Leibold & R.D. Holt, (Eds). 2005. *Metacommunities: Spatial Dynamics and Ecological Communities*. University Chicago Press, 520 p.
- Honnay, O. & Bossuyt, B. 2005. Prolonged clonal growth: escape route or route to extinction? *Oikos* 108: 427-432.
- Honnay, O., Hermý, M. & Coppin, P. 1999. Effects of area, age and diversity of forest patches in Belgium on plant species richness, and implications for conservation and reforestation. *Biol. Conserv.* 87: 73-84.
- Honnay, O., Jacquemyn, H., Bossuyt, B., & Hermý, M. 2005. Forest fragmentation effects on patch occupancy and population viability of herbaceous plant species. *New. Phytol.* 166: 723-736.
- Hooftman, D.A.P., J.G.B. Oostermeijer & J.C.M. Den Nijs 2006. Invasive behaviour of *Lactuca serriola* (Asteraceae) in The Netherlands: spatial distribution and ecological amplitude. *Basic and Applied Biology* 7: 507-519.
- Hooper, DU, Chapin FS, Ewel JJ, Hector A et al. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecol. Monogr.* 75: 3-35.
- Hosmer, D.W. & Lemeshow S. 1999. *Applied survival analysis: Regression modeling of time to event data*. Wiley series in probability and statistics. John Wiley & sons, inc.
- Howe, H.F. & Smallwood, J. 1982. Ecology of seed dispersal. *Ann. Rev. Ecol. Syst.* 13: 201-228.
- Hubbell, S.P. & Foster, R.B. 1992. Short-term dynamics of a Neotropical forest: why ecological research matters to tropical conservation and management. *Oikos* 63: 48-61.
- Hubbell, S.P. & R.B. Foster 1986. Commonness and rarity in a neotropical forest: implications for tropical tree conservation. In: M.E. Soulé (ed.): *Conservation biology; The science of scarcity and diversity*, pp. 205-231.
- Hubbell, S.P. 1997. A unified theory of biogeography and relative species abundance and its application to tropical rain forests and coral reefs. *Coral Reefs* 16: 9-21.
- Hubbell, S.P. 2001: The unified neutral theory of biodiversity and biogeography. *Monographs in Population Biology* 32: 1-375. Princeton Univ. Press.
- Hubbell, S.P. 2005. Neutral theory in community ecology and the hypothesis of functional equivalence. *Funct. Ecol.* 19: 166-172.
- Hubbell, S.P. 2006. Neutral theory and the evolution of ecological equivalence. *Ecology* 87: 1387-1398.
- Hubbell, S.P., Foster R.B., O'Brien S.T., et al. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science* 283: 554-557.
- Hughes, L., Dunlop, M., French, K., Leishman, M.R. et al. 1994. Predicting dispersal spectra: a minimal set of hypotheses based on plant attributes. *J. Ecol.* 82: 933-950.
- Huiskes, A.H.L., Koutslaal, B.P., Herman, P.M.J., Beefink, W.G. et al. 1995. Seed dispersal of halophytes in tidal marshes. *J. Ecol.* 83: 559-567.
- Huisman, J., & Weissing, F. 1999. Biodiversity of plankton by species oscillations and chaos. *Nature* 402: 407-410.
- Huisman, J., Olff H. & Fresco L.F.M. 1993. A hierarchical set of models for species response analysis. *J. Veg. Sci.* 4: 37-46.
- Hunt, R. & Cornelissen, J.H.C. 1997. Components of relative growth rate and their interrelations in 59 temperate plant species. *New Phytol.* 135: 395-417.
- Hunt, R., Hodgson, J.G., Thompson, K. et al. 2004. A new practical tool for deriving a functional signature for herbaceous vegetation. *Appl. Veg. Sci.* 7: 163-170.
- Huntly, N.J. 1991. Herbivores and the dynamics of communities and ecosystems. *Ann. Rev. Ecol. Syst.* 22: 477-503.
- Husband, B.C. & S.C.H. Barrett. 1996. A metapopulation perspective in plant population biology. *J. Ecol.* 84: 461-469.
- Huston, M.A. & D.L. DeAngelis. 1994. Competition and coexistence: the effects of resource transport and supply rates. *Am. Nat.* 144: 954-977.
- Huston, M.A. 1994. *Biological diversity. The coexistence of species on changing landscapes*. Cambridge Univ. Press, Cambridge.
- Huston, M.A. 1999. Local processes and regional patterns: appropriate scale for understanding variation in the diversity of plants and animals. *Oikos* 86: 393-401.
- Hutchings, M.J. & Booth K.D. 1996. Studies on the feasibility of re-creating chalk grassland vegetation on erable land. I. The potential role of the seed bank and the seed rain. *J. Appl. Ecol.* 33: 1171-1181.
- Hutchinson, G.E. 1961. The paradox of the plankton. *Am. Nat.* 95: 137-145.
- IUCN, 2006. *The 2006 IUCN Red List of threatened species*. International Union for Conservation of Nature and Natural Resources (<http://www.iucnredlist.org/>).
- Jacquemyn, H., J. Butaye & M. Hermý. 2003. Impacts of restored patch density and distance from natural forests on colonization success. *Restoration Ecology* 11: 417-423.
- Jager, S.W. 1985. A prehistoric route and ancient cart-tracks in the Gemeente of Anloo (Province of Drenthe). *Palaeohistoria* 27: 185-242.
- Jakobsson, A. & Eriksson, O. 2000. A comparative study of seed number, seed size, seedling size and recruitment in grassland plants. *Oikos* 88: 494-502.
- Jansen, A.J.M., Fresco L.F.M., Grootjans A.P. & Jalink M.H. 2004. Effects of restoration measures on plant communities of wet heathland ecosystems. *Appl. Veg. Sci.* 7: 243-252.
- Jansen, P.A., F. Bongers & L. Hemerik, 2004. Seed mass and mast seeding enhance dispersal by a neotropical scatter-hoarding rodent. *Ecol. Monogr.* 74: 569-589.

- Jansson, R, Zinko U, Merritt DM, Nilsson C 2005. Hydrochory increases riparian plant species richness: a comparison between a free-flowing and a regulated river. *J. Ecol.* 93: 1094-1103.
- Jansson, R., C. Nilsson & B. Renöfält. 2000. Fragmentation of riparian floras in rivers with multiple dams. *Ecology* 81: 899-903.
- Janzen, D.H. & P.S. Martin. 1982. Neotropical anachronisms: The fruits the Gomphotheres ate. *Science* 215: 19-27.
- Janzen, D.H. 1982. Differential seed survival and passage rates in cows and horses, surrogate pleistocene dispersal agents. *Oikos* 38: 150-156
- Janzen, D.H. 1984. Dispersal of small seeds by big herbivores: foliage is the fruit. *Am. Nat.* 123: 338-353.
- Janzen, D.H. 1988. Management of Habitat Fragments in a Tropical Dry Forest: Growth. *Annals of the Missouri Botanical Garden* 75: 105-116.
- Jenkowska-Blaszczuk, M. & Grubb, P.J. 1997. Soil seed banks in primary and secondary deciduous forest in Białowieża, Poland. *Seed Sci. Res.* 7: 281-292.
- Joenje, W. 1978. *Plant colonization and succession on embanked sandflats*. PhD-thesis, University of Groningen.
- Johansson, M.E. & Nilsson, C. 1993. Hydrochory, population dynamics and distribution of the clonal aquatic plant *Ranunculus lingua*. *J. Ecol.* 81: 81-91.
- Jongejans, E. & Schippers, P. 1999. Modelling seed dispersal by wind in herbaceous species. *Oikos* 87: 362-372.
- Jongejans, E. & Telenius, A. 2001. Field experiments on seed dispersal by wind in ten umbelliferous species (Apiaceae). *Plant Ecol.* 152: 67-78.
- Jongman, R.H.G., Ter Braak, C.J.F. and Van Tongeren, O.F.R. 1995. *Data analysis in community and landscape ecology*. Second edition. - Pudoc, Wageningen, The Netherlands, Reissued in 1995 by Cambridge University Press, 299 pp.
- Jordano, P. 2000. Fruits and frugivory. In: M. Fenner (ed.) *Seeds - The Ecology, of regeneration in plant communities*, pp. 125-161. 2nd edition. CAB International.
- Kahmen, S. & Poschlod, P. 2004. Plant functional trait responses to grassland succession over 25 years. *J. Veg. Sci.* 15: 21-32.
- Kalamees, R. & M. Zobel. 2002. The role of the seed bank in gap regeneration in a calcareous grassland community. *Ecology* 83: 1017-1025.
- Kalweit, H. (ed.). 1993. *The Rhine under the influence of man. – River engineering works, shipping, water management*. Internationale Kommission für die Hydrologie des Rheingebietes. Berichte Nr. I-11. [In German with English summary].
- Kareiva, P. & U. Wennnergren. 1995. Connecting landscape patterns to ecosystem and population processes. *Nature* 373: 299-302
- Katenhusen, O. 2001. Die Ausbreitung von Pflanzen durch Hochwasser in norddeutschen Flusslandschaften. *Zeitschrift für Ökologie und Naturschutz* 9: 225-236.
- Katul, G.G., Porporato A., Nathan R., et al. 2005. Mechanistic analytical models for long-distance seed dispersal by wind. *Am. Nat.* 166: 368-381
- Kearns, C.A., Inouye, D.W. & Waser, N.M. 1998. Endangered mutualisms: The conservation of plant-pollinator interactions. *Ann. Rev. Ecol. Syst.* 29: 83-112.
- Keddy, P., K. Nielsen, E. Weiher & R. Lawson. 2002. Relative competitive performance of 63 species of terrestrial herbaceous plants. *J. Veg. Sci.* 13: 5-16.
- Keddy, P.A. 1992. Assembly and response rules: two goals for predictive community ecology. *J. Veg. Sci.* 3: 157-164.
- Kelt, D.A., Tarper, M.L. & Meserve, P.L. 1995. Assessing the impact of competition on community assembly: a case study using small mammals. *Ecology* 76: 1283-1296.
- Kempski, E. 1906. *Über endozoische Samenverbreitung und speziell die Verbreitung von Unkräutern durch Tiere auf dem Wege des Darmkanals*. PhD-thesis University of Rostock, 170 pp. [in German].
- Keymer, J.E., P.A. Marquet, J.X. Velasco-Hernández & S.A. Levins. 2000. Extinction thresholds and metapopulation persistence in dynamic landscapes. *Am. Nat.* 156: 478-494.
- Kirmer, A., S. Tischew, W.A. Ozinga, M. von Lampe & J.M. van Groenendaal. 2008. Importance of regional species pools and functional traits in colonisation processes. *J. Appl. Ecol.* [in revision].
- Kiviniemi, K. & Eriksson, O. 1999. Dispersal, recruitment and site occupancy of grassland plants in fragmented habitats. *Oikos* 86: 241-253.
- Kiviniemi, K. & Telenius, A. 1998. Experiments on adhesive dispersal by wood mouse: seed shadows and dispersal distances of 13 plant species from cultivated areas in southern Sweden. *Ecography* 21: 108-116.
- Kiviniemi, K. 1996. A study of adhesive seed dispersal of three species under natural conditions. *Acta Bot. Neerl.* 45: 73-83.
- Klapp, E. 1971. *Wiesen und Weiden. Eine Grünlandlehre*. Vierte Auflage. Paul Parey, Berlin/Hamburg. [in German].
- Klapp, E., Boeker, P., König, F. & Stählin, A. 1953. *Wertzahlen der Grünlandpflanzen*. Grünland 2: 38-40. [in German].
- Kleijn, D & W.J. Sutherland. 2003. How effective are European agri-environment schemes in conserving and promoting biodiversity? *J Appl. Ecol.* 40: 947-969.
- Kleijn, D., Berendse F, Smit R. & Gilissen N. 2001. Agri-environment schemes do not effectively protect biodiversity in Dutch agricultural landscapes. *Nature* 413: 723-725.
- Kleyer, M. 1999. The distribution of plant functional types on gradients of disturbance intensity and resource supply in an agricultural landscape. *J. Veg. Sci.* 10: 679-708.

- Kleyer, M. 2002. Validation of plant functional types across two contrasting landscapes. *J. Veg. Sci.* 13: 167-178.
- Kleyer, M., R.M. Bekker, I.C. Knevel, J.P. Bakker, K. Thompson et al. The LEDA Traitbase: A database of life-history traits of Northwest European flora. *J. Ecol.* (Submitted)
- Klimeš, L. & Klimesová, J. 1999. CLO-PLA2 - a database of clonal plants in central Europe. *Plant Biol.* 141: 9-19.
- Klimeš, L. 1999. Small-scale plant mobility in a species-rich grassland. *J. Veg. Sci.* 10: 209-218.
- Klimeš, L., J. Klimešová, R. Hendriks & J.M. Van Groenendaal 1997. Clonal plant architectures: a comparative analysis of form and function. In: H. de Kroon & J. van Groenendaal (Eds.): *The ecology and evolution of clonal plants*, pp. 1-29. Backhuys Publishers, Leiden, the Netherlands, 453 pp.
- Klinkhamer, P.G.L., De Jong, T.J., Metz, J.A.J. & Val, J. 1987. Life history tactics of annual organisms: the joint effects of dispersal and delayed germination. *Theor. Pop. Biol.* 32:127-156.
- Kloos, A.W. 1939. Nederlandse wol-adventieven. *De Levende Natuur* 43: 275-279, 328-342, 372-376. [in Dutch].
- Klotz, S., I. Kühn & W. Durka, Eds. 2004. BIOLFLOR – Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. *Schriftenreihe für Vegetationskunde* 38: 1-334.
- Kneitel, J.M. & Chase, J.M. 2004. Trade-offs in community ecology: linking spatial scales and species coexistence. *Ecol. Lett.* 7: 69-80.
- Knevel, I.C. 1997. *The role of seed attributes in predicting seed longevity*. MSc-thesis UFZ - Centre for Environmental Research, Leipzig-Halle Ltd. / Groningen University.
- Knevel, I.C., Bekker, R.M., Bakker, J.P. & Kleyer, M. 2003. Life-history traits of the Northwest European flora: A data-base (LEDa). *J. Veg. Sci.* 14: 611-614.
- Knevel, I.C., R.M. Bekker, D. Kunzmann, M. Stadler, K. Thompson (Eds.). 2005. *The LEDA Traitbase Collecting and Measuring Standards of Life-history Traits of the Northwest European Flora*. University of Groningen, Community and Conservation Ecology Group; Scholma Druk B.V., Bedum. Also available at <http://www.leda-traitbase.org/standards.jsp>
- Knight, A.P. & Walter R.G. (Eds.). 2003. *A Guide to Plant Poisoning of Animals in North America*. International Veterinary Information Service, Ithaca NY.
- Kolar, C.S. & D.M. Lodge. 2001. Progress in invasion biology: predicting invaders. *Trends Ecol. Evol.* 16: 199-204.
- Kolb, A. & Diekmann M. 2004. Effects of environment, habitat configuration and forest continuity on the distribution of forest plant species. *J. Veg. Sci.* 15: 199-208.
- Kollmann, J. & B. Schneider. 1999. Landscape structure and diversity of fleshy-fruited species at forest edges. *Plant Ecology* 144: 37-48.
- Kollmann, J. 1995. Regeneration window for fleshy-fruited plants during scrub development on abandoned grassland. *Ecoscience* 2: 213-222.
- Kollmann, J. 2000. Dispersal of fleshy-fruited species: a matter of spatial scale? *Perspect. Plant Ecol. Evol. Syst.* 3: 29-51.
- Konold, W. 1997. Wässerwiesen, Wölbäcker, Hackäcker: Geschichte und Vegetation alter Kulturlandschaftselemente in Südwestdeutschland. *Verh. Gesell. Ökol.* 27: 53-61. [in German].
- Kunin, W.E. Extrapolating species abundance across spatial scales. 1998. *Science* 281: 1513-1515.
- Kupferschmid, A.D., Stampfi A. & Newberry D.M. 2000. Dispersal and microsite limitation in an abandoned calcareous grassland of the Southern Prealps. *Folia Geobot.* 35: 125-141.
- Lande, R. 1988. Genetics and demography in biological conservation. *Science* 241: 1455-1460.
- Lavorel, S. & Garnier, E. 2002. Predicting changes in community composition and ecosystem functioning from plant traits - revisiting the Holly Grail. *Funct. Ecol.* 16: 545-556.
- Lavorel, S., S. McIntyre, J. Landsberg & T.D.A. Forbes. 1997. Plant functional classification: from general groups to specific groups based on response to disturbance. *Trends Ecol. Evol.* 12: 474-478.
- Lawes Agricultural Trust, 2002. *GenStat for Windows* - 6th edition. IACR-Rothamsted, UK.
- Lawton, J.H. & R.M. May (eds.) 1995. *Extinction rates*. Oxford Univ. Press, Oxford.
- Lawton, J.H. 1999. Are there general laws in ecology? *Oikos* 84: 177-192.
- Legendre, P., Dale M.R.T., Fortin M.-J. et al. 2002. The consequences of spatial structure for the design and analysis of ecological field surveys. *Ecography* 25: 601-615.
- Leibold, M.A., M. Holyoak, M. Mouquet et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecol. Lett.* 7: 601-613.
- Leishman, M.R., Westoby M. 1998. Seed size and shape are not related to persistence in soil in Australia in the same way as in Britain. *Funct. Ecol.* 12: 480-485.
- Leishman, M.R. 1999. How well do plant traits correlate with establishment ability? Evidence from a study of 16 calcareous grassland species. *New Phytol.* 141: 487-496.
- Leishman, M.R., I.A. Wright, A.T. Moles & M. Westoby. 2000. The evolution ecology of seed size. In: M. Fenner (ed.): *Seeds: The ecology of regeneration in plant communities*, 2nd edn., pp. 31-57, CAB Int.
- Lennartz, H. 1957. Über die Beeinflussung der Keimfähigkeit der Samen von Grünlandpflanzen beim Durchgang durch den Verdauungstrakt des Rindes. *Zeitschrift Acker- Pflanzenbau* 103: 427-453. [in German].
- Lepš, J. & Šmilauer, P. 2003. *Multivariate analysis of ecological data using CANOCO*. - Cambridge University Press. 269 pp.
- Lepš, J. 2001. Species-pool hypothesis: limits to its testing. *Folia Geobot.* 36: 45-52.

- Lepš, J. 2004. What do the biodiversity experiments tell us about consequences of plant species loss in the real world? *Basic Appl. Ecol.* 5: 529-534.
- Levey, D.J. 1987. Seed size and fruit-handling techniques of avian frugivores. *Am. Nat.* 129: 471-485.
- Levin, S.A. 1992. The problem of pattern and scale in ecology. *Ecology* 73: 1943-1967.
- Levin, S.A. Cohen, D. & Hastings, A. 1984. Dispersal strategies in patchy environments. *Theoretical Population Biology* 26: 165-191.
- Levine, J.M. & D.J. Murrell. 2003. The community-level consequences of seed dispersal patterns. *Ann. Rev. Ecol. Syst.* 34: 549-574.
- Levine, J.M. & M. Rees. 2002. Coexistence and relative abundance in annual plant assemblages: The roles of competition and colonisation. *Am. Nat.* 160: 452-467.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Entomol. Soc. Am.* 15: 237-240.
- Leyer, I. 2006. Dispersal, diversity and distribution patterns in pioneer vegetation: The role of river-floodplain connectivity. *J. Veg. Sci.* 17: 407-416.
- Lindborg, R. & O. Eriksson. 2004. Historical landscape connectivity affects present plant species diversity. *Ecology* 85: 1840-1845.
- Lockwood, J.L. & Pimm S.L. 1999. When does restoration succeed? In: Weiher E. & Keddy P.A. (eds.), *Ecological assembly rules. Perspectives, advances, retreats*. Cambridge Univ. Press. Pp. 363-378.
- Lockwood, J.L., Cassey, P., & Blackburn, T. 2005. The role of propagule pressure in explaining species invasion. *Trends Ecol. Evol.* 20: 223-228.
- Lohmeyer, W. & H. Sukopp. 1992. Agriophyten in der Vegetation Mitteleuropas. *Schriftenr. Vegetationskd.* 25, Bonn-Bad Godesberg. [In German]
- Loreau, M. & N. Mouquet. 1999. Immigration and the maintenance of local species diversity. *Am. Nat.* 154: 427-440.
- Loreau, M. 2000. Are communities saturated? On the relationship between alpha, beta and gamma diversity. *Ecol. Lett.* 3: 73-76.
- Loreau, M. 2000. Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos* 91: 3-17.
- Loreau, M., N. Mouquet & A. Gonzalez. 2003. Biodiversity as spatial insurance in heterogeneous landscapes. *Proc. Natl. Acad. Sci. U.S.A.* 100: 12765-12770.
- Loreau, M., N. Mouquet & R.D. Holt. 2003. Meta-ecosystems: a theoretical framework for a spatial ecosystem ecology. *Ecology Letters* 6: 673-679.
- Lucassen, E.C.H.E.T., A.J.P. Smolders, L.P.M. Lamers & J.G.M. Roelofs. 2005. Water table fluctuations and groundwater supply are important in preventing phosphate-eutrophication in sulphate-rich fens: Consequences for wetland restoration. *Plant Soil* 269: 109-115.
- Luick, R. & E.M. Bignal. 2002. The significance of EU agricultural policy on the nature conservation of pastoral landscapes. In: B. Redecker, P. Finck, W. Härdtle, U. Riecken & E. Schröder (eds.): *Pastoral landscapes and nature conservation*. Springer-Verlag. Pg. 329-346.
- Lundberg, J. & F. Moberg. 2003. Mobile link organisms and ecosystem functioning: implications for ecosystem resilience and management. *Ecosystems* 6: 87-98.
- Lytle, D.A. & N.L. Poff. 2004. Adaptation to natural flow regimes. *Trends Ecol. Evol.* 19: 95-100.
- MacArthur, R.H. & Connell, J.H. 1966. *The biology of populations*. J. Wiley, New York.
- MacArthur, R.H. & Wilson, E.O. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, N.Y.
- Macdonald, G.M. 1993. Fossil pollen analysis and the reconstruction of plant invasions. *Adv. Ecol. Res.* 24: 67-110.
- Maes, N.C.M. & C.J.A. Rôvekamp. 1997. *Oorspronkelijk inheemse houtige gewassen in Drenthe*. Provincie Drenthe, Assen.
- Magri, D., G.G. Vendramin, B. Comps et al. 2006. A new scenario for the Quaternary history of European beech populations: palaeobotanical evidence and genetic consequences. *New Phytol.* 171: 199-221.
- Magurran, A.E. 2005. Species abundance distributions: pattern or process? *Funct. Ecol.* 19: 177-181.
- Malanson, G.P. & Armstrong, M.P. 1996. Dispersal probability and forest diversity in a fragmented landscape. *Ecological Modelling* 87: 91-102.
- Malo, J. E., Suarez, F. 1995. Herbivorous mammals as seed dispersers in a Mediterranean dehesa. *Oecologia* 104: 246-255.
- Malo, J.E. & Suarez, F. 1995. Establishment of pasture species on cattle dung: the role of endozoochorous seeds. *J. Veg. Sci.* 6: 169-174.
- Malo, J.E., Jimenez, B. & Suarez, F. 1995. Seed bank build-up in small disturbances in a Mediterranean pasture: the contribution of endozoochorous dispersal by rabbits. *Ecography* 18: 73-82.
- Manzano, P. & J.E. Malo. 2006. Extreme long-distance seed dispersal via sheep. *Front. Ecol. Environm.* 4: 244-248.
- Matejková, I., Van Diggelen, R. & Prach, K. 2003. An attempt to restore a central European species-rich mountain grassland through grazing. *Appl. Veg. Sci.* 6: 161-168.
- Matlack, G.R. 1987. Diaspore size shape and fall behaviour in wind-dispersed plant species. *Am. J. Bot.* 74: 1150-1160.
- Matlack, G.R. 2005. Slow plants in a fast forest: local dispersal as a predictor of species frequencies in a dynamic landscape. *J. Ecol.* 93: 50-59.
- Mayfield, M., M. Boni, G. Daily, D.D. Ackerly. 2005. Species and functional diversity of native and human-dominated plant communities. *Ecology* 86: 2365-2372.

- McCullagh, P. & Nelder, J.A. 1989. *Generalized Linear Models*. 2nd edition. - Chapman & Hall, London.
- McCune, B. 1994. Improving community analysis with Beals smoothing function. *Ecoscience* 1: 82-86.
- McCune, B. 1997. Influence of noisy environmental data on canonical correspondence analysis. - *Ecology* 78: 2617-2623.
- McGill, B.J. 2003. A test of the unified neutral theory of biodiversity. *Nature* 422: 881-885.
- McGill, B.J. 2003. Strong and weak tests of macroecological theory. *Oikos* 103: 679-685.
- McGill, B.J., B.A. Maurer & M.D. Weiser. 2006. Empirical evaluation of neutral theory. *Ecology* 87: 1411-1423.
- McLachlan, J.S., J.S. Clark, P.S. Manos 2005. Molecular indicators of tree migration capacity under rapid climate change. *Ecology* 86: 2088-2098.
- Menges, E.S. 2000. Population viability analyses in plants: challenges and opportunities. *Trends Ecol. Evol.* 15: 51-56.
- Meyer, S.E. & Carlson, S.L. 2001. Achene mass variation in *Ericmeria nauseosus* (Asteraceae). in relation to dispersal ability and seedling fitness. *Funct. Ecol.* 15: 274-281.
- Meziane, D., & Shipley B. 1999. Interacting components of interspecific relative growth rate: constancy and change under differing conditions of light and nutrient supply. *Funct. Ecol.* 13: 611-622
- Middleton, B. 2000. Hydrochory, seed banks, and regeneration dynamics along the landscape boundaries of a forested wetland. *Plant Ecol.* 146: 169-184.
- Milberg, P. & Lamont, B.B. 1997. Seed/cotyledon size and nutrient content play a major role in early performance of species on nutrient-poor soils. *New Phytol.* 137: 665-672.
- Millennium Ecosystem Assessment, 2005. *Ecosystems and human well-being: The biodiversity synthesis report*. Island Press, Washington, DC.
- Milton, S.J. & Dean, W.R.J. 2001. Seeds dispersed in dung of insectivores and herbivores in semi-arid southern Africa. *J. Arid Environm.* 47: 465-483.
- Milton, S.J. 2003. Emerging ecosystems: a washing-stone for ecologists, economists and sociologists? *South African Journal of Science* 99: 404-406.
- Milton, S.J., W.R. Siegfried & W.R.J. Dean. 1990. The distribution of epizoochoric plant species: a clue to the prehistoric use of arid Karoo rangelands by large herbivores. *J. Biogeogr.* 17: 25-34.
- Minami, S. & Azuma, A. 2003. Various flying modes of wind-dispersal seeds. *J. Theor. Biol.* 225: 1-14.
- Mix, C. 2006. *The population genetics of plant species in fragmented landscapes*. PhD thesis Radboud University Nijmegen.
- MNP, 2007. *Ecologische evaluatie regelingen voor natuurbeheer. Programma beheer en Staatsbosbeheer 2000-2006*. MNP, Bilthoven. [Ecological evaluation of Dutch nature policy]
- Moles, A.T, Hodson D.W, Webb C.J. 2000. Do seed size and shape predict persistence in soil in New Zealand? *Oikos* 89: 541-545.
- Moles, A.T. & M. Westoby. 2004. Seedling survival and seed size: a synthesis of the literature. *J. Ecol.* 92: 372-383.
- Moles, A.T. & M. Westoby. 2006. Seed size and plant strategy across the whole life cycle. *Oikos* 113: 91-105.
- Moles, A.T., Ackerly D.D., Webb C.O., et al. 2005. Factors that shape seed mass evolution. *Proc. Natl. Acad. Sci. U.S.A.* 102: 10540-10544.
- Moles, A.T., Ackerly, D.D., Tweddle, J.C., Dickie et al. 2007. Global patterns in seed size. *Global Ecol. Biogeogr.* 16:109-116.
- Moles, A.T., Falster D.S., Leishman M.R. & Westoby M. 2004. Small-seeded species produce more seeds per square metre of canopy per year, but not per individual per lifetime. *J. Ecol.* 92: 384-396.
- Mouissie, A.M., C.E.J. van der Veen, G. F. Veen & R. van Diggelen. 2005. Ecological correlates of seed survival after ingestion by Fallow Deer. *Funct. Ecol.* 19: 284-290.
- Mouissie, A.M., P. Vos, H.M.C. Verhagen & J.P. Bakker. 2005. Endozoochory by free-ranging, large herbivores: Ecological correlates and perspectives for restoration. *Basic Appl. Ecol.* 6: 547-558.
- Mouissie, A.M., W. Lengkeek & R. van Diggelen. 2005. Estimating adhesive seed-dispersal distances: field experiments and correlated random walks. *Funct. Ecol.* 19: 478-486.
- Mouquet, N. & M. Loreau, M. 2002. Coexistence in metacommunities: the regional similarity hypothesis. *Am. Nat.* 159: 420-426.
- Mouquet, N. & M. Loreau. 2003. Community patterns in source-sink metapopulations. *Am. Nat.* 162: 544-557.
- Mouquet, N., Leady P., Meriguet J. & Loreau M. 2004. Immigration and local competition in herbaceous plant communities: a three-year seed-sowing experiment. *Oikos* 104: 77-90.
- Mrotzek, R., Halder, M. & Schmidt, W. 1999. Die Bedeutung von Wildschweinen für die diasporenausbreitung von Phanerogamen. *Verh. Gesell. Ökol.* 29: 437-443. [in German].
- Mucina M. 2001. *Ecosystems of Europe*. Encyclopedia of Biodiversity 2: 635-647.
- Muller-Landau, H.C., Levin, S.A. & Keymer, J.E. 2003. Theoretical perspectives on evolution of long-distance dispersal and the example of specialized pests. *Ecology* 84: 1957-1967.
- Müller-Schneider, P. 1983 Verbreitungsbiologie (Diasporologie) der Blütenpflanzen. *Veröff. Geobot. Inst. Eidg. Tech. Hochsch. Stift. Rübel Zür.* 61: 1-226. [in German].
- Müller-Schneider, P. 1986. Verbreitungsbiologie der Blütenpflanzen Graubündens. *Veröff. Geobot. Inst. Eidg Tech. Hochsch. Stift. Rübel Zür.* 85: 1-263. [in German].
- Münzbergová, Z. & Herben T. 2004. Identification of suitable unoccupied habitats in metapopulation studies using co-occurrence of species. *Oikos* 105: 408-414.

- Myers, J.A., Vellend, M., Gardescu, S. & Marks, P.L. 2004. Seed dispersal by white-tailed deer: implications for long-distance dispersal, invasion, and migration of plants in eastern North America. *Oecologia* 139: 35-44.
- Nagelkerke, C.J., J. Verboom, F. van den Bosch & K. van de Wolfshaar. 2002. Time lags in metapopulation responses to landscape change. In: K.J. Gutzwiller (ed.): *Applying landscape ecology in biological conservation*, pp. 330-354. Springer.
- Nathan, R. & Muller-Landau, H.C.M. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends Ecol. Evol.* 15: 278-285.
- Nathan, R. 2005. Long-distance dispersal research: building a network of yellow brick roads. *Diversity Distrib.* 11: 125-130.
- Nathan, R. 2006. Long-distance dispersal of plants. *Science* 313: 786-788.
- Nathan, R., Katul G.G. 2005. Foliage shedding in deciduous forests lifts up long-distance seed dispersal by wind. *Proc. Natl. Acad. Sci. U.S.A.* 102: 8251-8256.
- Nathan, R., Katul, G.G., Horn et al. 2002. Mechanisms of long-distance dispersal of seeds by wind. *Nature* 418: 409-413.
- Nathan, R., Sapir, N., Trakhtenbrot, A. et al. 2005. Long-distance biological transport processes through the air: can nature's complexity be unfolded in-silico? *Diversity Distrib.* 11: 131-137.
- Nee, S. & May, R.M. 1997. Extinction and the loss of evolutionary history. *Science* 278: 692-694.
- Nee, S. & N. Colegrave. 2006. Paradox of the clumps. *Nature* 441: 417-418.
- Nienhuis, P.H. & R.S.E.W. Leuven. 2001. River restoration and flood protection: controversy or synergism? *Hydrobiologica* 444: 85-99.
- Nilsson, C., Reidy CA, Dynesius M, Revenga C. Fragmentation and flow regulation of the world's large river systems. *Science* 308: 405-408.
- Nilsson, C., Andersson, E., Merrit, D.M. & Johansson, M.E. 2002. Differences in riparian flora between river-banks and river lakeshores explained by dispersal traits. *Ecology* 83: 2878-2887.
- Nilsson, C., Gardfjell, M. & Grelsson, G. 1991. Importance of hydrochory in structuring plant communities along rivers. *Can. J. Bot.* 69: 2631-2633.
- Noble, I.R. & Gitay, H. 1996. A functional classification for predicting the dynamics of landscapes. *J. Veg. Sci.* 7: 329-336.
- Oba, S., Furutani, T. & Fujimoto, F. 2000. Pod-shedding habit in *Medicago* species, evaluated by breaking strength of pedicels. *Field Crops Res.* 66: 269-276.
- Oborny, B. & Bartha, S. 1995. Clonality in plant communities - an overview. *Abstr. Bot.* 19: 115-127.
- Oke, T.R. 1987. *Boundary Layer Climates*, 2nd edition. Methuen, London.
- Økland, R.H. 1995. Persistence of vascular plants in a Norwegian boreal coniferous forest. *Ecography* 18: 3-14.
- Økland, R.H. 1999. On the variation explained by ordination and constrained ordination axes. *J. Veg. Sci.* 10: 131-136.
- Olden, J.D., LeRoy Poff, N. et al. 2004. Ecological and evolutionary consequences of biotic homogenization. *Trends Ecol. Evol.* 19: 18-24.
- Olff, H. & Bakker, J.P. 1991. Long-term dynamics of standing crop and species composition after cessation of fertilizer application to mown grasslands. *J. Appl. Ecol.* 28: 1040-1052.
- Olff, H. & M.E. Ritchie. 1998. Herbivore effects on grassland plant species richness. *Trends Ecol. Evol.* 13: 261-265.
- Olff, H. & M.E. Ritchie. 2002. Fragmented nature: consequences for biodiversity. *Landscape and Urban Planning* 58: 83-92.
- Olff, H., D.M. Pegtel, J.M. van Groenendael & J.P. Bakker. 1994. Germination strategies and vegetation structure during grassland succession. *J. Ecol.* 82: 69-79.
- Olff, H., Vera, F.W.M., Bokdam, J., Bakker, E.S. et al. 1999. Shifting mosaics in grazed woodlands driven by alternation of plant facilitation and competition. *Plant Biol.* 1: 127-137.
- Olivieri, I., Y. Michalakakis & P.H. Gouyon. 1995. Metapopulation genetics and the evolution of dispersal. *Am. Nat.* 146: 202-228.
- Opdam, P. & D. Wascher. 2004. Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. *Biol. Conserv.* 117: 285-297.
- Opdam, P., J. Verboom & R. Pouwels 2003. Landscape cohesion: an index for the conservation potential of landscapes for biodiversity. *Landscape Ecology* 18: 113-126.
- Opdam, P., R. Foppen & C. Vos. 2002. Bridging the gap between ecology and spatial planning in landscape ecology. *Landscape Ecology* 16: 767-779.
- Ouborg, N.J. & O. Eriksson. 2004. Towards a metapopulation concept for plants. In: Hanski, I. & O.E. Gaggiotti (eds.): *Ecology, genomics, and evolution of metapopulations*. Elsevier Ac. Press, Amsterdam.
- Ouborg, N.J. 1993. Isolation, population size and extinction: the classical and metapopulation approaches applied to vascular plants along the Dutch Rhine-system. *Oikos* 66: 298-308.
- Ouborg, N.J., Piquot Y., Van Groenendael J.M. 1999. Population genetics, molecular markers and the study of dispersal in plants. *J. Ecol.* 87: 551-568.
- Ouborg, N.J., P. Vergeer, & C. Mix. 2006. The rough edges of the conservation genetics paradigm for plants. *J. Ecol.* 94: 1233-1248.
- Özer, Z. & Hasimoglu, S. 1977. Preservation of Germination Ability of Some Weed Seeds Passed Through the Gastro Intestinal Tract of Sheep. *Turk. J. Phytopathol.* 6: 105-110.

- Özer, Z. 1979. Über die Beeinflussung der Keimfähigkeit der Samen mancher Grünlandpflanzen beim Durchgang durch den Verdauungstrakt des Schafes und nach Mistgärung. *Weed Research* 19: 247-254. [in German].
- Ozinga, W.A. & J.H.J. Schaminée 2004. The development of ecological information systems, a new tool in biological research. In: *Recent Res. Devel. Environ. Biol.* pg. 531-551.
- Ozinga, W.A. & J.H.J. Schaminée 2005. *Target species – Species of European concern. A data-base driven selection of plant and animal species for the implementation of the Pan European Ecological Network*. Wageningen, Alterra, Alterra-report 1119.
- Ozinga, W.A. S.M. Hennekens, J.H.J. Schaminée et al. 2005a. Assessing the relative importance of dispersal in plant communities using an ecoinformatics approach. *Folia Geobot.* 40: 53-68.
- Ozinga, W.A., J. van Andel & M.P. McDonnell-Alexander. 1997. Nutritional soil heterogeneity and mycorrhizas as determinants of plant species diversity. *Acta Bot. Neerl.* 46: 237-254.
- Ozinga, W.A., J.H.J. Schaminée, R.M. Bekker et al. 2005b. Predictability of plant species composition from environmental conditions is constrained by dispersal limitation. *Oikos* 108: 555-561.
- Ozinga, W.A., M. Bakkenes & J.H.J. Schaminée (2007). Sensitivity of Dutch vascular plants to climate change and habitat fragmentation; A preliminary assessment based on plant traits in relation to past trends and future projections. Wettelijke Onderzoekstaken Natuur & Milieu, *WOT-report* 49, Netherlands Environmental Assessment Agency.
- Ozinga, W.A., R.M. Bekker, J.H. J. Schaminée & J.M. Van Groenendael, 2004. Dispersal potential in plant communities depends on environmental conditions. *J. Ecol.* 92: 767-777.
- Ozinga, W.A., S.M. Hennekens, J.H.J. Schaminée, N.A.C. Smits et al. 2007. Local aboveground persistence of vascular plants: Life-history trade-offs and environmental constraints. *J. Veg. Sci.* 18: 489-497.
- Pakeman, R.J. 2001. Plant migration rates and seed dispersal mechanisms. *J. Biogeogr.* 28: 795-800.
- Pakeman, R.J., Attwood, J.P. & Engelen, J. 1998. Sources of plants colonising experimentally disturbed patches in an acidic grassland, in eastern England. *J. Ecol.* 86: 1032-1041.
- Pakeman, R.J., Digneffe, G. & Small, J.L. 2002. Ecological correlates of endozoochory by herbivores. *Funct. Ecol.* 90: 296-304.
- Pakeman, R.J., Engelen, J. & Attwood, J.P. 1999. Rabbit endozoochory and seedbank build-up in an acidic grassland. *Plant Ecol.* 145: 83-90.
- Palmer, M.W. & Rusch, G.M. 2001. How fast is the carousel? Direct indices of species mobility with examples from an Oklahoma grassland. *J. Veg. Sci.* 12: 305-318.
- Palmer, M.W. 1993. Putting things in even better order: the advantages of canonical correspondence analysis. *Ecology* 74: 2215-2230.
- Pandolfi, J.M. 2006. Corals fail a test of neutrality. *Nature* 440: 35-36.
- Pärtel, M. & M. Zobel 2007. Dispersal limitation may result in the unimodal productivity-diversity relationship: a new explanation for a general pattern. *J. Ecol.* 95: 90-94.
- Pärtel, M., Zobel M., Zobel K., & Van Der Maarel E. 1996. The species pool and its relation to species richness: evidence from Estonian plant communities. *Oikos* 75: 111-117.
- Peco, B., L. Lopez-Merino & M. Alvir 2006. Survival and germination of Mediterranean grassland species after simulated sheep ingestion: ecological correlates with seed traits. *Acta Oecol.* 30: 269-275.
- Peet, R.K., Knox, R.G., Case, J.S. & Allen, R.B. 1988. Putting things in order: the advantage of detrended correspondence analysis. - *Am. Nat.* 131: 924-934.
- Pegtel, D.M., J.P. Bakker, G.L. Verweij & L.F.M. Fresco. 1996. N, K and P deficiency in chronosequential cut summer-dry grasslands on gley podzol after cessation of fertilizer application. *Plant and Soil* 178: 121-131.
- Pérez-Barbería, F.J., Elston, D.A., Gordon, I.J. & Illius, A.W. 2004. The evolution of phylogenetic differences in the efficiency of digestion of ruminants. *Proc. R Soc.Lond. B Biol. Sci.* 271: 1081-1090.
- Persson, S. 1981. Ecological indicator values as an aid in the interpretation of ordination diagrams. *J. Ecol.* 69:71-84.
- Petit, R.J., et al. 2002 Identification of refugia and post-glacial colonization routes of European white oaks based on chloroplast DNA and fossil pollen evidence. *For. Ecol. Manage.* 156: 49-74.
- Petrak, M. 1987. Futterwertzahl und Beäussungsintensität ausgewählter Nahrungspflanzen des Damhirsches (*Cervus dama* L.). *Zeitschrift für Jagdwissenschaft* 33: 98-105. [In German]
- Pimm, S., H.L. Jones & J. Diamond. 1988. On the risk of extinction. *Am. Nat.* 132: 757-785.
- Pimm, S.L., Russell, G.J., Gittleman, J.L. & Brooks, T.M. 1995. The future of biodiversity. *Science*, 269, 347-350.
- Pitelka, L.F., et al. 1997. Plant migration and climate change. *American Scientist* 85: 464-473.
- Pollux, B.J.A., L. Santamaria & N. J. Ouborg. 2005. Differences in endozoochorous dispersal between aquatic plant species, with reference to plant population persistence in rivers. *Freshw. Bio.* 50: 232-242.
- Pons, T.L. 1989. Breaking seed dormancy by nitrate as gap detecting mechanism. *Ann. Bot.* 63: 139-143.
- Poorter, L. 2007. Are species adapted to their regeneration niche, adult niche, or both? *Am. Nat.* 169: 433-442.
- Poschlod, P. & S. Bonn. 1998. Changing dispersal processes in the central European landscape since the last ice age: an explanation for the actual decrease of plant species richness in different habitats? *Acta Bot. Neerl.* 47: 27-44.
- Poschlod, P. 1993. Die Dauerhaftigkeit von generativen Diasporenbanken in Böden von Kalkmagerrasenpflanzen und deren Bedeutung für den botanischen Arten- und Biotopschutz. *Verh. Gesell. Ökol.* 22: 229-240.
- Poschlod, P., J.P. Bakker & S. Kahmen. 2005. Changing land use and its impact on biodiversity. *Basic Appl. Ecol.* 6: 93-98.

- Poschlod, P., J.P. Bakker, S. Bonn & S. Fischer. 1996. Dispersal of plants in fragmented landscapes. In: Settele, J., C.R. Margules, P. Poschlod & K. Henle (Eds.): *Species survival in fragmented landscapes*. Kluwer, Dordrecht, pp. 123-12.
- Poschlod, P., Kleyer, M. & Tackenberg, O. 2000. Databases on life history traits as a tool for risk assessment in plant species. *Zeitschrift für Ökologie und Naturschutz* 9: 3-18.
- Poschlod, P., S. Kiefer, U. Tränkle, S. Fischer & S. Bonn. 1998. Plant species richness in calcareous grasslands as affected by dispersability in space and time. *Appl. Veg. Sci.* 1: 75-90.
- Pott, R. 1995. The origin of grassland plant species and grassland communities in Central Europe. *Fitosociologia* 29: 7-32.
- Pott, R. 2000. Palaeoclimate and vegetation - long-term vegetation dynamics in central Europe with particular reference to beech. *Phytocoenologia* 30: 285-333.
- Prach, K., Pyšek P. & Šmilauer P. 1993. On the rate of succession. *Oikos* 66: 343-346.
- Praeger, R.L. 1913. On the buoyancy of the seeds of some Britannic plants. *Sci. Proc. R. Dubl. Soc.* 14: 13-62.
- Preston, C.D., D.A. Pearman & T.D. Dines. 2002. *New Atlas of the British and Irish Flora*. Oxford University Press, Oxford.
- Preston, F.W. 1948. The commonness, and rarity, of species. *Ecology* 3: 254-283.
- Preston, F.W. 1962. The canonical distribution of commonness and rarity. *Ecology* 43: 185-215, 410-432.
- Prinzing, A., Durka, W., Klotz, S. & Brandl, R. 2002. Geographic variability of ecological niches of plant species – are competition and stress relevant? *Ecography* 25: 721-729.
- Prinzing, A., W.A. Ozinga & W. Durka 2004. The relationship between global and regional distribution diminishes among phylogenetically basal species. *Evolution* 58: 2622 – 2633.
- Proctor, V.W. 1968. Long-distance dispersal of seeds by retention in digestive tracts of birds. *Science* 160: 321-322.
- Provenza, F.D., J.J. Villalba, L.E. Dziba, S.B. Atwood & R.E. Banner. 2003. Linking herbivore experience, varied diets, and plant biochemical diversity. *Small Ruminant Research* 49: 257-274.
- Pulliam, H.R. 1988. Sources, sinks, and population regulation. *Am. Nat.* 132: 652-661.
- Purves, D.W. & Pacala, S.W. 2005. Ecological drift in niche structured communities: neutral pattern does not imply neutral processes. In: *Biotic Interactions in the Tropics* (eds Burslem, D., Pinard, M. & Hartley, S.). Cambridge University Press, Cambridge, pp. 107-138.
- Purvis, A. & Rambaut, A. 1995. *Comparative Analysis of Independent Contrasts (CAIC): A Statistical Package for the Apple Macintosh, Version 2.0 User's Guide*. (Oxford University Press, Oxford).
- Rabinowitz, D. 1981. Seven forms of rarity. In: H. Singe (ed): *The biological aspects of rare plant conservation*. Rackham, O., 1986. *The history of the countryside; the full fascinating story of Britain's landscape*. Dent, London.
- Recknagel, F. 2006. *Ecological Informatics: Scope, Techniques and Applications*. 2nd edition. Springer, 496 pp.
- Rees, M. 1993. Trade-offs among dispersal strategies in British plants. *Nature* 366: 150-152.
- Rees, M. 1996. Evolutionary ecology of seed dormancy and seed size. *Phil. Trans. R. Soc. Lond. B* 351: 1299-1308.
- Rees, M., R. Condit, M. Crawley, S. Pacala & D. Tilman. 2001. Long-term studies of vegetation dynamics. *Science* 293: 650-655.
- Reich, P.B., Walters, M.B., Ellsworth, D.S., Vose, J.M., Volin, J.C. & Bowman, W.D. 1999. Generality of leaf trait relationships: a test across six biomes. *Ecology* 80: 1955-1969.
- Remmert, H. 1991. *The mosaic cycle concept of ecosystems*. Ecological Studies 85. Springer Verslag, Berlin.
- Renes, J., 1997. *Landschappen van Maas en Peel: geschiedenis, kenmerken en waarden van het cultuurlandschap van Noord- en Midden-Limburg*. DLO Rapport 192: 1-573.
- Richards, P.W. & A.R. Clapham 1941. *Juncus effusus* L. *J. Ecol.* 29: 375-380
- Ricklefs, R. 1987. Community diversity: relative roles of local and regional processes. *Science* 235: 167-171.
- Ricklefs, R.E. & Schluter D. 1993. Species diversity, regional and historical influences. In: Ricklefs R.E. & Schluter D. (eds.), *Species diversity in ecological communities*, pp. 350-363.
- Ridley, H.N. 1930. *The dispersal of plants throughout the world*. L. Reeve & Co., Ltd.
- Ritchie, M.E. & Olff, H. 1999. Spatial scaling laws yield a synthetic theory of biodiversity. *Nature* 400: 557-560.
- Rodwell, J.S., J.H.J. Schaminée, L. Mucina et al. 2002. *The diversity of European vegetation*. An overview of phytosociological alliances and their relationship to EUNIS habitats. EC-LNV-rapport 2002/054, Wageningen, 168 pp.
- Roelofs, J.G.M., E. Brouwer & R. Bobbink. 2002. Restoration of aquatic macrophyte vegetation in acidified and eutrophicated shallow soft water wetlands in the Netherlands. *Hydrobiologia* 478: 171-180.
- Roelofs, J.G.M., R. Bobbink, E. Brouwer & M.C.C. De Graaf. 1996. Restoration ecology of aquatic and terrestrial non-calcareous sandy soils in The Netherlands. *Acta Bot. Neerl.* 45: 517-541.
- Romell, L.G. 1938. Växternas spridningsmöjligheter. *Växternas* 4: 279-448.
- Römermann, C. 2006. Patterns and processes of plant species frequency and life-history traits. *Dissertationes Botanicae* 402: 1-117.
- Römermann, C., Tackenberg, O. & Poschlod, P. 2005. How to predict attachment potential of seeds to sheep and cattle coat from simple morphological traits. *Oikos* 110: 219-230.
- Rosenzweig, M.L. & Ziv Y. 1999: The echo pattern of species diversity: pattern and processes. *Ecography* 22: 614-628.
- Rosenzweig, M.L. 1995. *Species diversity in space and time*. Cambridge Univ. Press, Cambridge, UK.
- Ruiz, M. & J.P. Ruiz. 1986. Ecological history of transhumance in Spain. *Biol. Conserv.* 37: 73-86.

- Rural European Platform, 2007. <http://www.ruraleuropeanplatform.org/rep.html> (17-05-2006)
- Russi, L., Cocks, P.S. & Roberts, E.H. 1992. The fate of legume seeds eaten by sheep from a Mediterranean grassland. *J. Appl. Ecol.* 29: 772-778.
- Sala, O.E., F.S. Chapin, J.J. Armesto et al. 2000. Biodiversity - global biodiversity scenarios for the year 2100. *Science* 287: 1170-1174.
- Salisbury, E.J. 1933. *The influence of man on vegetation*. Trans. S.E. Union Sci. Soc. 1933, 1-17.
- Salisbury, E.J. 1942. *On the reproductive capacity of plants*. Bell, London, UK.
- Salisbury, E.J. 1952. *Downs & dunes. Their plant life and its environment*. G. Bell & Sons, Ltd, London. 328 pp.
- Salisbury, E.J. 1953. A changing flora as shown in the study of weeds of arable land and water places. In: J.E. Lousely (ed.) *The changing flora of Britain*. pp. 130-139.
- Salisbury, E.J. 1961. *Weeds and aliens*. Collins St James's place, London.
- Salisbury, E.J. 1974. Seed size and mass in relation to environment. *Proc. R. Soc. Lond. B Biol. Sci.* 186: 83-88.
- Saverimutta, T. & Westoby, M. 1996. Components of variation in seedling potential growth rate: phylogenetically independent contrasts. *Oecologia* 105: 281-285.
- Schaffers, A.P. & Sýkora, K.V. 2000. Reliability of Ellenberg indicator values for moisture, nitrogen and soil reaction: a comparison with field measurements. *J. Veg. Sci.* 11: 225-244.
- Schaminée, J.H.J., Hommel, P.W.F.M., Stortelder, A.H.F., Weeda, E.J. & Westhoff, V. 1995-1999. *De Vegetatie van Nederland*, Vols. 1-5. - Opulus Press, Uppsala/Leiden. [In Dutch].
- Schaminée, J.H.J., S.M. Hennekens & W.A. Ozinga, 2007. Use of the ecological information system SynBioSys for the analysis of large datasets. *J. Veg. Sci.* 18: 463-470.
- Schaminée, J.H.J., Van Kley, J.E. & Ozinga, W.A. 2002. The analysis of long-term changes in plant communities: case studies from the Netherlands. *Phytocoenologia* 32: 317-335.
- Scheffer, M. & E.H. van Nes. 2006. Self-organized similarity, the evolutionary emergence of groups of species. *Proc. Natl. Acad. Sci. U.S.A.* 103: 6230-6235.
- Schemske, D.W., B.C. Husband, M.H. Ruckelshaus et al. 1994. Evaluating approaches to the conservation of rare and endangered plant species. *Ecology* 75: 584-606.
- Schmidt, M., Sommer, K., Kriebitzsch, W.-U. et al. 2004. Dispersal of vascular plants by game in northern Germany. Part I: Roe Deer (*Capreolus capreolus*) and Wild Boar (*Sus scrofa*). *Eur. J. For. Res.* 123: 167-176.
- Schneider, R.L. & Sharitz, R.R. 1988. Hydrochory and regeneration in a bald cypress-water tupelo swamp forest. *Ecology* 69: 1055-1063.
- Schrijver, R.A.M., W.A. Ozinga & W.H. Diemont, 2007. Payments for pastoral landscapes of Europe. In A.P. Grootjans & L. Wolejko (editors). Multifunctional use of Polish peatlands. In press.
- Schrijver, R.A.M., P.B.M. Berentsen, R.A. Groeneveld et al. 2006. Development of nature-oriented dairy farm systems with an optimization model: the case of 'Farming for Nature' in 'de Langstraat', the Netherlands. *Agrarwirtschaft* 55: 280-289.
- Schulz, B., Döring, J. & Gottsberger, G. 1990. Apparatus for measuring the fall velocity of anemochorous diaspores, with results from two plant communities. *Oecologia* 86: 454-456.
- Seabloom, E.W., Harpole W.S., Reichman O.J. & D. Tilman. 2003. Invasion, competitive dominance, and resource use by exotic and native California grassland species. *Proc. Natl. Acad. Sci. U.S.A.* 100: 13384-13389.
- SER, 2004. *The SER International Primer on Ecological Restoration*. www.ser.org & Tucson: Society for Ecological Restoration International.
- Shaffer, M.L. 1981. Minimal population sizes for species conservation. *BioScience* 31: 131-134.
- Sheldon, J.C. & Burrows, F.M. 1973. The dispersal effectiveness of the achene-pappus units of selected Compositae in steady winds with convection. *New Phytol.* 72: 665-675.
- Shipley, B. & Dion, J. 1992. The allocation of seed production in herbaceous angiosperms. *Am. Nat.* 139: 467-483.
- Shipley, B., D. Vile & E. Garnier. 2006. From plant traits to plant communities: A statistical mechanistic approach to biodiversity. *Science* 314: 812-814.
- Shmida, A. & Ellner, S. 1983. Seed dispersal on pastoral grazers in open Mediterranean chaparral, Israel. *Isr. J. Bot.* 32: 147-159.
- Shmida, A. & Ellner, S. 1984. Coexistence of plant species with similar niches. *Vegetatio* 58, 29-55.
- Silvertown, J. 2004. Plant coexistence and the niche. *Trends Ecol. Evol.* 19: 605-611.
- Silvertown, J. 2005. *Demons in Eden: The paradox of plant diversity*. University of Chicago Press.
- Silvertown, J., M.E. Dodd, D.J.G. Gowing & J.O. Mountford. 1999. Hydrologically defined niches reveal a basis for species richness in plant communities. *Nature* 400: 61-63.
- Silvertown, J., McConway, K.J., Hughes, Z. et al. 2002. Ecological and genetic correlates of long-term population trends in the park grass experiment. *Am. Nat.* 160: 409-420.
- Simberloff, D. 2004. Community ecology: Is it time to move on? *Am. Nat.* 163: 787-799.
- Sipe, T.W. & A.R. Linnerooth 1995. Intraspecific Variation in Samara Morphology and Flight Behavior in *Acer saccharinum* (Aceraceae). *Am. J. Bot.* 82: 1412-1419.
- Skeate, S.T. 1987. Interactions between birds and fruits in a northern Florida hammock community. *Ecology* 68: 297-309.
- Skoglund, S.J. 1990. Seed dispersing agents in two regularly flooded river sites. *Can. J. Bot.* 68: 754-760.
- Slichter Van Bath, B. H. 1980. *The Agrarian History Of Western Europe, A.D. 500-1850*, Spectrum, Utrecht [English translation by Olive Ordish].

- Smart, S.M., Bunce R.G.H., Firbank L.G., et al. 2002. Do field boundaries act as refugia for grassland plant species diversity in intensively managed agricultural landscapes in Britain? *Agr. Ecosyst. Env.* 91: 73-87.
- Smits, N.A.C., Schaminee J.H.J., van Duuren L. 2002. 70 years of permanent plot research in The Netherlands. *Appl. Veg. Sci.* 5: 121-126.
- Snow, B. & Snow, D. 1988. *Birds and berries. A study of an ecological interaction*. Poyser, Calthor.
- Soons, M.B. & Heil, G.W. 2002. Reduced colonization capacity in fragmented populations of wind-dispersed grassland forbs. *J. Ecol.* 90: 1033-1043.
- Soons, M.B. & W.A. Ozinga 2005. How important is long-distance seed dispersal for the regional survival of plant species? *Diversity and Distributions* 11: 165-172.
- Soons, M.B., Heil G.W., Nathan R., Katul G.G. 2004a. Determinants of long-distance seed dispersal by wind in grasslands. *Ecology* 85: 3056-3068.
- Soons, M.B., Messelink J.H., Jongejans E., & Heil G.W. 2005. Habitat fragmentation reduces grassland connectivity for both short-distance and long-distance wind-dispersed forbs. *J. Ecol.* 93: 1214-1225.
- Soons, M.B., Nathan, R. & Katul, G.G. 2004b. Human effects on long-distance wind dispersal and colonization by grassland plants. *Ecology* 85: 3069-3079.
- Sorensen, A.E. 1986. Seed dispersal by adhesion. *Annu. Rev. Ecol. Syst.* 17: 443-463.
- Southwood, T.R.E. 1988. Tactics, strategies and templets. *Oikos* 52: 3-18.
- Spehn, E.M., Hector A., Joshi J. et al. 2005. Ecosystem effects of biodiversity manipulations in European grasslands. *Ecol. Monogr.* 75: 37-63.
- Spek, T. 2004. *Het Drentse esdorpenlandschap: een historisch-geografische studie*. PhD thesis, University of Wageningen. Matrijs, Utrecht. [In Dutch with English summary]
- Stadler, M., D. Ahlers, R.M. Bekker et al. 2006. Web-based tools for data analysis and quality assurance on a life-history trait database of plants of Northwest Europe. *Environmental Modelling & Software* 21: 1536-1543.
- Stearns, S.C. 1992. *The evolution of life histories*. Oxford Univ. Press, Oxford.
- Stebbins, G.L. 1971. Adaptive radiation of reproductive characteristics in angiosperms. II. Seeds and seedlings. *Annu. Rev. Ecol. Syst.* 2: 237-260.
- Stender, S., Poschlod, P., Vauk-Henzelt, E. & Dernerde, T. 1997. Die Ausbreitung durch Galloway-Rinder. *Verhandlungen der Gesellschaft für Ökologie* 27: 173-180.
- Stevens, C. & I.D. Hume. 1995. *Comparative physiology of the vertebrate system*. Cambridge Univ. Press.
- Stevens, C.J., Dise N.B., Mountford J.O., Gowing D.J. 2004. Impact of nitrogen deposition on the species richness of grasslands. *Science* 303: 1876-1879.
- Stiles, E.W. 1992. Animals as seed dispersers. In: M. Fenner (ed.) *Seeds - The Ecology, of regeneration in plant communities*. CAB International. pp. 87-104.
- Stortelder, A.H.F., R.A.M. Schrijver, I.M. van den Top & H. Alberts, 2001. *Boeren voor natuur. Scenario's voor het landelijk gebied*. Alterra-rapport 279, Wageningen.
- Strykstra, R.J., Bekker R.M., Bakker J.P. 1998. Assessment of dispersule availability: its practical use in restoration management. *Acta Bot. Neerl.* 47: 57-70.
- Strykstra, R.J., Bekker R.M., Van Andel J. 2002. Dispersal and life span spectra in plant communities: a key to safe site dynamics, species coexistence and conservation. *Ecography* 25: 145-160.
- Strykstra, R.J., Pegtel, D.M. & Bergsma, A. 1998. Dispersal distance and achene quality of the rare anemochorous species *Arnica montana* L.: implications for conservation. *Acta Bot. Neerl.* 47: 45-56.
- Stuart, A.J. 1991. Mammalian extinctions in the Late Pleistocene of northern Eurasia and North America. *Biological Reviews* 66: 453-562.
- Stuart, A.J. 2005. The extinction of woolly mammoth (*Mammuthus primigenius*) and straight-tusked elephant (*Palaeoloxodon antiquus*) in Europe. *Quaternary International* 126-28: 171-177.
- Suding, K.N., Collins S.L., Gough L. et al. 2005. Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. *Proc. Natl. Acad. Sci. U.S.A.* 102: 4387-4392.
- Suding, K.N., D.E. Goldberg & K.M. Hartman. 2003. Relationships among species traits: separating levels of response and identifying linkages to abundance. *Ecology* 84: 1-16.
- Suding, K.N., K.L. Gross & G.R. Houseman. 2004. Alternative states and positive feedbacks in restoration ecology. *Trends Ecol. Evol.* 19: 46-53.
- Sutherland, G.D., Harestad, A.S., Price, K. & Lertzman, K.P. 2000. Scaling of natal dispersal distance in terrestrial birds and mammals. *Conserv. Ecology* 4, 16: <http://www.consecol.org/vol4/iss1/art16>.
- Sutherland, W.J. 2002. Openness in management. *Nature* 418: 834-835.
- Sutherland, W.J., A.S. Pullin, P.M. Dolman & T.M. Knight. 2004. The need for evidence-based conservation. *Trends Ecol. Evol.* 19: 305-308.
- Svenning, J.-C. & F. Skov. 2004. Limited filling of the potential range in European tree species. *Ecol. Lett.* 7: 565-573.
- Sykes, M.T., Van der Maarel, E., Peet, R.K. & Willems, J.H. 1994. High species mobility in species-rich plant communities: an international comparison. *Folia Geobot. Phytotax.* 29: 439-448.
- Sýkora, K.V., E. Scheper & F. van der Zee, 1988. Inundation and the distribution of plant communities on Dutch river dikes. *Acta Bot. Neerl.* 37: 279-290.
- Tack, G., P. van den Brecht & M. Hermy. 1993. *Bossen van Vlaanderen. Een historische ecologie*. Uitgeverij Davidsfonds, Leuven. [In Dutch]

- Tackenberg, O. 2001. *Methoden zur Bewertung gradueller Unterschiede des Ausbreitungspotentials von pflanzenarten - Modellierung des Windausbreitungspotentials und regelbasierte Ableitung des Fernausbreitungspotentials*. PhD thesis Marburg University. [In German]
- Tackenberg, O. 2003. Modelling long-distance dispersal of plant diaspores by wind. *Ecol. Monogr.* 73: 173-189.
- Tackenberg, O., Poschod, P. & Bonn, S. 2003. Assessment of wind dispersal potential in plant species. *Ecol. Monogr.* 73: 191-205.
- Tamis, W.L.M. & Van 't Zelfde, M. 2003. The KFK-scale, a new rarity scale for the Dutch flora. *Gorteria* 29: 57-83. [In Dutch with English summary].
- Tamis, W.L.M. Changes in the Flora of the Netherlands in the 20th Century. PhD thesis University of Leiden. (Gorteria Supplement 6, National Herbarium Nederland, Leiden, 2005).
- Tamis, W.L.M., M. van 't Zelfde, R. van der Meijden & H.A. Udo de Haes. 2005. Changes in vascular plant biodiversity in the Netherlands in the 20th century explained by their climatic and other environmental characteristics. *Climatic Change* 72: 37-56.
- Tamis, W.L.M., Van 't Zelfde, M. & Van der Meijden, R. et al. 2005. Ecological interpretation of changes in the dutch flora in the 20th century. *Biol. Conserv.* 125: 211-224
- Tamm, C.O. 1956. Further observations on the survival and flowering of some perennial herbs: I. *Oikos* 7: 273-292.
- Tansley, A.G. 1935. The use and abuse of vegetation concepts and terms. *Ecology* 16: 284-307.
- Telfer, M.G., Preston, C.D. & Rothery, P. 2002. A general method for measuring relative change in range size from biological atlas data. *Biol. Cons.* 107: 99-109.
- Temperton, V.M, R.J. Hobbs, T. Nuttle & S. Halle (eds.) 2004. *Assembly Rules and Restoration Ecology: Bridging the Gap Between Theory and Practice*. Island Press, Washington, D.C., 439 pp.
- Ter Braak, C.J.F. & A.P. Schaffers. 2004. Co-correspondence analysis: A new ordination method to relate two community compositions. *Ecology* 85: 834-846.
- Ter Braak, C.J.F. & P. Šmilauer. 2002. *CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (version 4.5)*. Microcomputer Power (Ithaca NY, USA), 500 pp.
- Ter Braak, C.J.F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67: 1167-1179.
- Thellung, A. 1912. La flore adventice de Montpellier. *Mem. Soc. Nation. Sci. Nat. Math.* 38: 57-728. [In French]
- Theobald, D.M., N.T. Hobbs, T. Bearly et al. 2000. Incorporating biological information in local land-use decision making: designing a system for conservation planning. *Landsc. Ecol.* 15: 35-45.
- Thissen, P.H.M. & M. Meijer, 1991. Rug- en hangbouwbevoeiing in Nederland; een negentiende-eeuwse cultuurtechnische innovatie die niet doorzette. *Landinrichting* 31: 16-22. [In Dutch]
- Thomas, C.D. & Abery, J.C.G. 1995. Estimating rates of butterfly decline from distribution maps: the effects of scale. *Biol. Cons.* 73, 59-65.
- Thomas, C.D., A. Cameron, R.E. Green et al. 2004. Extinction risk from climate change. *Nature* 427: 145-148.
- Thompson, K, A.P. Askew, J.P. Grime et al. 2005. Biodiversity, ecosystem function and plant traits in mature and immature plant communities. *Funct. Ecol.* 19: 355-358.
- Thompson, K. & Baster, K. 1992. Establishment from seed of selected Umbelliferae in unmanaged grassland. *Funct. Ecol.* 6: 346-352.
- Thompson, K. & Hodgkinson, D.J. 1998. Seed mass, habitat and life history: a re-analysis of Salisbury 1942, 1974. *New Phytol.* 138: 163-167.
- Thompson, K. 1994. Predicting the fate of temperate species in response to human disturbance and global change. *Biodiversity, Temperate Ecosystems, and Global Change* (ed. by T.J.B. Boyle and C.E.B. Boyle), pp. 61-76. Springer-Verlag, Berlin.
- Thompson, K., Bakker, J.P. & Bekker, R.M. 1997. The soil seed banks of north west Europe: methodology, density and longevity, pp. 1-276. Cambridge University Press, Cambridge.
- Thompson, K., Bakker, J.P., Bekker, R.M. & Hodgson, J.G. 1998. Ecological correlates of seed persistence in soil in the north-west European flora. *J. Ecol.* 86: 163-169.
- Thompson, K., Ceriani, R.M., Bakker, J.P. & Bekker, R.M. 2003. Are seed dormancy and persistence in soil related? *Seed Sci. Res.* 13: 97-100.
- Thompson, K., Gaston, K.J. & Band, S.R. 1999. Range size, dispersal and niche breadth in the herbaceous flora of central England. *J. Ecol.* 87: 150-155.
- Thompson, K., Grime, J.P. & Mason, G. 1977. Seed germination in response to diurnal fluctuations in temperature. *Nature* 267: 147-148.
- Thompson, K., Hodgson, J.P. Grime, J.P. et al. 1993. Ellenberg numbers revisited. *Phytocoenologia* 23: 277-289.
- Thompson, K., Rickard, L.C., Hodgkinson, D.C. & Rees, M. 2002. Seed dispersal: the search for trade-offs. In: Bullock, J.M., Kenward, R.E. & Hails, R.S. (eds) *Dispersal Ecology*, pp. 152-172. Blackwell Publishing, Oxford.
- Tilman, D, J. Hill, C. Lehman. 2006. Carbon-negative biofuels from low-input high-diversity grassland biomass. *Science* 314: 1598-1600.
- Tilman, D. & C.L. Lehman 1997. Habitat destruction and species extinctions. In: D. Tilman & P. Kareiva (eds): *Spatial ecology. The role of space in population dynamics and interspecific interactions*. Princeton Univ. Press, New Jersey. Pp. 233-249
- Tilman, D. 1985. The resource ratio hypothesis of succession. *Am. Nat.* 125: 827-852.

- Tilman, D. 1990. Constraints and tradeoffs: towards a predictive theory of competition and succession. *Oikos* 58: 3-15.
- Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75: 2-16.
- Tilman, D. 1997. Community invasibility, recruitment limitation and grassland biodiversity. *Ecology* 78: 81-92.
- Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* 80: 1455-1474.
- Tilman, D. 2004. Niche tradeoffs, neutrality, and community structure: A stochastic theory of resource competition, invasion, and community assembly. *Proc. Natl. Acad. Sci. U.S.A.* 101: 10854-10861.
- Tilman, D., & Pacala, S. 1993. The maintenance of species richness in plant communities. In: R.E. Ricklefs, and Schluter, D. (eds.), *Species diversity in ecological communities*, pp. 13-25.
- Tilman, D., K.G. Cassman, P.A. Matson, R. Naylor & S. Polasky. 2002. Agricultural sustainability and intensive production practices. *Nature* 418: 671-677.
- Tilman, D., May, R.M., Lehman, C.L. & Nowak, M.A. 1994. Habitat destruction and the extinction debt. *Nature* 371: 65-66.
- Titus, J.E. & Hoover, D.T. 1991. Towards predicting reproductive success in submersed angiosperms. *Aquat. Bot.* 41: 111-136.
- Tjoelker, M.G., Craine, J.M., Wedin, D., Reich, P.B. & Tilman, D. 2005. Linking leaf and root trait syndromes among 39 grassland and savannah species. *New Phytol.* 167: 493-508.
- Tockner, K. & J.A. Stanford, 2002. Riverine flood plains: present state and future trends. *Env. Conserv.* 29: 308-330.
- Trakhtenbrot, A., Nathan, R., Perry, G. & Richardson, D.M. 2005. The importance of long-distance dispersal in biodiversity conservation. *Diversity Distrib.* 11: 173-181.
- Trexler, J.C. & Travis, J. 1993. Nontraditional regression analyses. *Ecology* 74: 1629-1637.
- Turnbull, L.A., Crawley, M.J. & Rees, M. 2000. Are plant populations seed-limited? A review of seed sowing experiments. *Oikos* 88: 225-238.
- Turnbull, L.A., L. Manley & M. Rees. 2005. Niches rather than neutrality, structure a grassland pioneer guild. *Proc. R. Soc. B.* 272: 1357-1364.
- Tüxen, R. 1937. Die Pflanzengesellschaften Nordwestdeutschlands. *Mitteilungen der floristisch-soziologischen Arbeitsgemeinschaft* 3: 1-170.
- United Nations, 2002. *Report of the World Summit on Sustainable Development, Johannesburg, South Africa*, 26 August-4 September 2002. Unated Nations, A/CONF.199/20, See http://www.unctad.org/en/docs/aconf199d20&c1_en.pdf.
- Valverde, T. & Silvertown, J. 1997. A metapopulation model for *Primula vulgaris*, a temperate forest understorey herb. *J. Ecol.* 85: 193-210.
- Van Andel, J. & J. Aronson. 2006. *Restoration Ecology*. Blackwell Publishing, Oxford. 319 pp.
- Van Andel, J. & J.P. van den Bergh. 1987. Disturbance of grasslands - outline of the theme. In: J. van Andel, J.P. Bakker & R.W. Snaydon (eds): *Disturbance in grasslands - causes, effects and processes*. Junk Publishers, Dordrecht, pp. 3-13.
- Van den Berg, L.J.L., Dorland E., Vergeer P. et al. 2005. Decline of acid-sensitive plant species in heathland can be attributed to ammonium toxicity in combination with low pH. *New Phytol.* 166: 551-564.
- Van den Broek, T., van Diggelen R., & Bobbink R. 2005. Variation in seed buoyancy of species in wetland ecosystems with different flooding dynamics. *J. Veg. Sci.* 16: 579-586.
- Van der Maarel, E. & M.T. Sykes. 1997. Rates of small-scale species mobility in alvar limestone grassland. *J. Veg. Sci.* 8: 199-208.
- Van der Maarel, E. & Sykes, M.T. 1993. Small-scale plant species turnover in a limestone grassland: the carousel model and some comments on the niche concept. *J. Veg. Sci.* 4: 179-188.
- Van der Maarel, E. 1972. Ordination of plant communities on the basis of their plant genus, family and order relationships. In: E. Van der Maarel & R. Tüxen (eds). *Grundlagen und Methoden in der Pflanzensoziologie*. Verslag W. Junk n.v., Den Haag.
- Van der Maarel, E. 1979. Multivariate methods in phytosociology, with reference to the Netherlands. In: M.J.A. Werger (red.), *The Study of Vegetation*. Junk, The Hague/Boston/London: 161-225.
- Van der Maarel, E. 1990. Ecotenes and ecoclines are different. *J. Veg. Sci.* 1: 135-138.
- Van der Maarel, E. 2005. *Vegetation Ecology* - an overview. In: E. van der Maarel (Ed.): *Vegetation Ecology*. Blackwell Publishing.
- Van der Meijden, R. 1996. *Heukels' flora van Nederland*. 22nd edition. Wolters-Noordhoff, Groningen.
- Van der Meijden, R., Odé, B., Groen, C.L.G., Witte, J.-P.M. & Bal, D. 2000. Endangered and Vulnerable Vascular Plants in the Netherlands. *Gorteria* 26: 85-208. [In Dutch with English summary].
- Van der Pijl, L. 1982. *Dispersal in higher plants*. 3rd edn. Springer, Berlin.
- Van Dorp, D., Schippers, P. & Van Groenendaal, J.M. 1997. Migration rates of grassland plants along corridors in fragmented landscapes assessed with a cellular automaton model. *Landscape Ecol.* 12: 39-50.
- Van Eck, W. H. J. M., J. P. M. Lenssen, H. M. van de Steeg, C. W. P. M. Blom & H. de Kroon. 2006. Seasonal dependent effects of flooding on plant species survival and zonation: a comparative study of 10 terrestrial grassland species. *Hydrobiologia* 565: 59-69.
- Van Eck, W.H.J.M., van de Steeg H.M., Blom C.W.P.M. & de Kroon H. 2005. Recruitment limitation along disturbance gradients in river floodplains. *J. Veg. Sci.* 16: 103-110.

- Van Eck, W.H.J.M., van de Steeg H.M., Blom C.W.P.M. & de Kroon H. 2004. Is tolerance to summer flooding correlated with distribution patterns in river floodplains? A comparative study of 20 terrestrial grassland species. *Oikos* 107: 393-405.
- Van Groenendaal, J.M., Ehrlén, J. & Svensson, B.M. 2000. Dispersal and persistence: population processes and community dynamics. *Folia Geobot.* 35: 107-114.
- Van Groenendaal, J.M., Klimes, L., Klimešová, J. & Hendriks, R. 1997. Comparative ecology of clonal plants. *Phil. Trans. R. Soc. Lond. B* 351: 1331-1339.
- Van Groenendaal, J.M., N.J. Ouborg & R.J.J. Hendriks. 1998. Criteria for the introduction of plant species. *Acta Bot. Neerl.* 47: 3-13.
- Van Leeuwen, C.G. 1966. A relation theoretical approach to pattern analysis. *Wentia* 15: 25-46.
- Van Ruijven, J. & F. Berendse, 2005. Diversity-productivity relationships: Initial effects, long-term patterns, and underlying mechanisms. *Proc. Natl. Acad. Sci. U.S.A.* 102 (3): 695-700.
- Van Steenis, C.G.G.J. 1925. Over phanerogamen en vaatkryptogamen voorkomende op knotwilgen in Nederland. *Nederlands Kruidkundig Archief* 1925: 361-406. [in Dutch]
- Van Steenis, C.G.G.J. 1928. Over phanerogamen en vaatkryptogamen voorkomende op knotwilgen in Nederland. Tweede stuk. *Nederlands Kruidkundig Archief* 1928: 52-58. [in Dutch]
- Van Tongeren, O. 2004. The identification programme ASSOCIA. In Hennekens 1998-2004: Turboveg for Windows.
- Van Tongeren, O., Gremmen, N.J.M. & Hennekens, S.M. 2007. Assignment of relevés to pre-defined classes by supervised clustering of plant communities using a new composite index. *J. Veg. Sci.* (in press).
- Van Wieren, S.E. 1996. Digestive strategies in ruminants and non-ruminants. PhD-thesis University of Wageningen.
- Vellend, M., Verheyen K, Jacquemyn H, et al. 2006. Extinction debt of forest plants persists for more than a century following habitat fragmentation. *Ecology* 87: 542-548.
- Venable, D.L. & Brown, J.S. 1988. The selective interaction of dispersal, dormancy and seed size as adaptations for reducing risks in variable environments. *Am. Nat.* 131: 360-384.
- Vera, F.W.M. 2000. *Grazing Ecology and Forest History*. CABI Publishing, 528 pp.
- Verboom, J, R. Foppen, P. Chardon P, P. Opdam & P. Luttikhuisen, 2001. Introducing the key patch approach for habitat networks with persistent populations: an example for marshland birds. *Biol. Cons.* 100: 89-101.
- Vergeer, P., L.J.L. van den Berg, J. Baar, N.J. Ouborg & J.G.M. Roelofs. 2006. The effect of turf cutting on plant and arbuscular mycorrhizal spore recolonisation - Implications for heathland restoration. *Biol. Conserv.* 129: 226-235.
- Vergeer, P., L.J.L. van den Berg, J.G.M. Roelofs, N.J. Ouborg. 2005. Single-Family versus Multi-Family Introductions. *Plant Biol.* 7: 509-515.
- Vergeer, P., Rengelink R., Ouborg N.J. & J.G.M. Roelofs 2003. Effects of population size and genetic variation on the response of *Succisa pratensis* to eutrophication and acidification. *J. Ecol.* 91: 600-609.
- Vergeer, P., Sonderen E. & Ouborg N.J. 2004. Introduction strategies put to the test: Local adaptation versus heterosis. *Cons. Biol.* 18: 812-821.
- Verhagen, R., Klooker J., Bakker J.P. 2001. Restoration success of low-production plant communities on former agricultural soils after top-soil removal. *Appl. Veg. Sci.* 4: 75-82.
- Villalba, J.J. & F.D. Provenza. 2005. Foraging in chemically diverse environments: energy, protein, and alternative foods influence ingestion of plant secondary metabolites by lambs. *J. Chem. Ecol.* 31: 123-137.
- Villalba, J.J., F.D. Provenza & G.-D. Han. 2004. Experience influences diet mixing by herbivores: implications for plant biochemical diversity. *Oikos* 107: 100-109.
- Violle, C., Navas M.-L., Vile D. et al. 2007. Let the concept of trait be functional! *Oikos* 116: 882-892.
- Vitousek, P.M., H.A. Mooney, J. Lubchenko & J.M. Melillo, 1997. Human domination of earth's ecosystems. *Science* 277: 494-499.
- Vleeshouwers, L.M., H.J. Bouwmeester & C.M. Karssen. 1995. Redefining seed dormancy: an attempt to integrate physiology and ecology. *J. Ecol.* 83: 1031-1037.
- Volkov, I., J.R. Banavar, F. He, S.P. Hubbell & A. Maritan. 2005. Density dependence explains tree species abundance and diversity in tropical forests. *Nature* 438: 658-661.
- Volkov, I., J.R. Banavar, S.P. Hubbell & A. Maritan. 2003. Neutral theory and relative species abundance in ecology. *Nature* 424: 1035-1037.
- Von Holle, B. & D. Simberloff. 2005. Ecological resistance to biological invasion overwhelmed by propagule pressure. *Ecology* 86: 3212-3218.
- Vos, C.C. & Zonneveld, J.I.S. 1993. *Patterns and processes in a landscape under stress: the study area. Landscape ecology of a stressed environment* (ed. by C.C. Vos and P. Opdam), pp. 1-28. Chapman & Hall, London.
- Vos, C.C., J. Verboom, P.F.M. Opdam & C.J.F. Ter Braak, 2001. Toward ecologically scaled landscape indices. *Am. Nat.* 157: 24-41
- Vos, W. & Stortelder, A.H.F. 1992. *Vanishing tuscan landscapes. Landscape ecology of a submediterranean-montane area (Solano Basin, Tuscany, Italy)*. Pudoc, wageningen.
- Wahaj, S.A., Levey, D.J., Sanders, A.K. & Cipollini, M.L. 1998. Control of gut retention time by secondary metabolites in ripe *Solanum* fruits. *Ecology* 79: 2309-2319.
- Wallis de Vries, M.F. 1995. Large herbivores and the design of large-scale nature reserves in Western-Europe. *Conserv. Biol.* 9: 25-33.

- Walter, K.S. & H.J. Gillett (eds.) 1998. 1997 IUCN Red List of Threatened Plants. Compiled by the World Conservation Monitoring Centre. IUCN, Gland, Switzerland and Cambridge, UK
- Wamelink, G.W.W., Goedhart P.W., Van Dobben H.F. & F. Berendse. 2005. Plant species as predictors of soil pH: Replacing expert judgement with measurements. *J. Veg. Sci.* 16: 461-470
- Wamelink, G.W.W., Joosten, V., Van Dobben, H.F. & Berendse, F. 2002. Validity of Ellenberg indicator values judged from physico-chemical field measurements. *J. Veg. Sci.* 13: 269-278.
- Wardle, D.A., Bardgett R.D., Klironomos J.N., et al. 2004. Ecological linkages between aboveground and below-ground biota. *Science* 304: 1629-1633.
- Wassen, M.J., H. Olde Venterink, E.D. Lapshina & F. Tanneberger. 2005. Endangered plants persist under phosphorus limitation. *Nature* 437: 547-550.
- Waterbolk, H.T. 1968. Food production in prehistoric Europe. *Science* 162: 1039-1102.
- Watkinson, A.R. 1992. Plant senescence. *Trends Ecol. Evol.* 7: 417-420.
- Watt, A.S. 1947. Pattern and process in the plant community. *J. Ecol.* 35: 1-22.
- Watt, A.S. 1960. Population-changes in acidiphilous grassheath in breckland, 1936-57. *J. Ecol.* 48: 605-629.
- Watts, W.A. 1988. Europe. In: B. Huntley and T. Webb III (eds): *Vegetation History*, pp.155-192. Kluwer Academic Press, Dordrecht, Netherlands.
- Webb, C.O. & D.R. Peart. 2001. High dispersal rates in faunally intact tropical rain forest: theoretical and conservation implications. *Ecol. Lett.* 4: 491-499.
- Wedderburn, R.W.M. 1974. Quasi-Likelihood functions, generalized linear models, and the Gauss-Newton Method. *Biometrika* 61: 439-447.
- Weeda, E.J. 1985-1994. *Nederlandse oecologische flora. Wilde planten en hun relaties*. 1-5. IVN, Amsterdam. [Dutch ecological flora; In Dutch]
- Weeda, E.J. 1997. Het goed recht van emotionele bezwaren. *De Levende Natuur* 98: 89.
- Weeda, E.J. 2001-2002. *Viola persicifolia* Schreber in the Netherlands in past and present. *Stratiotes* 23: 73-103; 24: 3-12. [in Dutch with English summary]
- Weeda, E.J. 2004. Boerendiversiteit voor biodiversiteit. *Alterra-rapport* 973 [in Dutch]
- Weeda, E.J., J.H.J. Schaminée & L. Van Duuren. 2000-2005. *Atlas of plant communities in the Netherlands*. Vol 1-4. KNNV Uitgeverij, Utrecht, The Netherlands. [in Dutch]
- Weeda, E.J., W.A. Ozinga & G.A.J.M. Jagers op Akkerhuis. 2006. Diversiteit hoog houden; Bouwstenen voor een geïntegreerd natuurbeheer. *Alterra-rapport* 1418. [In Dutch]
- Weiher, E. & P.A. Keddy. 1995. Assembly rules, nul models, and trait dispersion: new questions from old patterns. *Oikos* 74: 159-164.
- Weiher, E. & P.A. Keddy. 1995. The assembly of experimental wetland plant communities. *Oikos* 73: 232-335.
- Weiher, E. & P.A. Keddy. 1999. Relative abundance and evenness patterns along diversity and biomass gradients. *Oikos* 87: 355-361.
- Weiher, E., G.D.P. Clarke & P.A. Keddy. 1998. Community assembly rules, morphological dispersion, and the coexistence of plant species. *Oikos* 81: 309-322.
- Weiher, E., Van der Werf, A., Thompson, K. et al. 1999. Challenging Theophrastus: A common core list of plant traits for functional Ecology. *J. Veg. Sci.* 10: 609-620.
- Welch, D. 1985. Studies in the grazing of heather moorland in north-east Scotland. IV. Seed dispersal and plant establishment in dung. *J. Appl. Ecol.* 22: 46-72.
- Wenny, D.G. 2001. Advantages of seed dispersal: A re-evaluation of directed dispersal. *Evol. Ecol. Res.* 3: 51-74.
- Werner, P.A. & W.J. Platt. 1976. Ecological relationships of co-occurring goldenrods (*Solidago*: Compositae). *Am. Nat.* 110: 959-971.
- Westhoff, V. & E. Van der Maarel. 1978. The Braun-Blanquet approach. In: Whittaker, R.H. (Ed.): *Classification of plant communities*. 2nd ed., pp. 287-399.
- Westhoff, V. 1983. Man's attitude towards vegetation. In: W. Holzner, M.J.A. Werger & I. Ikusima (Eds.): *Man's impact on vegetation*, pp. 7-24. Junk, The Hague.
- Westhoff, V. 1994. Introductie van inheemse plantesoorten. *Natuurhistorisch Maandblad* 83: 170-174.
- Westoby, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant Soil* 199: 213-227.
- Westoby, M., Falster, D.S., Moles, A.T. et al. 2002. Plant ecological strategies: some leading dimensions of variation between species. *Annu. Rev. Ecol. Syst.* 33: 125-159.
- Westoby, M., Leishman, M. & Lord, J. 1996. Comparative Ecology, of seed size and seed dispersal. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 351: 1309-1318.

- Whitfield, J. 2006. How green was my subsidy? *Nature* 439: 908-909.
- Whittaker, C.R. 1988. *Pastoral economies in classical antiquity*. Cambridge Univ. Press.
- Whittaker, R.H. & S.A. Levin. 1977. The role of mosaic phenomena in natural communities. *Theoretical Population Biology* 12: 117-139.
- Whittaker, R.H. 1965. Dominance and diversity in plant communities. *Science* 147: 250-260.
- Whittaker, R.H. 1975. *Communities and ecosystems*. 2nd edition. Macmillan, New York.
- Whittaker, R.J., Willis, K.J. & Field, R. 2001. Scale and species richness, towards a general, hierarchical theory of species diversity. *J. Biogeogr.* 28: 453-470.
- Wieringa, J., Rijkooort, P.J. 1983. *Windklimaat van Nederland (Klimaat van Nederland 2)*. KNMI, Staatsuitgeverij, Den Haag.
- Wiese, H. 1966. Der Rinderhandel im nördwesteuropäischen Küstengebiet vom 15. Jahrhundert bis zum Beginn des 19. Jahrhundert. Stuttgart. [In German]
- Wilkinson, D.M. 1997. Plant colonization: are wind dispersed seeds really dispersed by birds at larger spatial and temporal scales? *J. Biogeogr.* 24: 61-65.
- Willson, M.F. 1993. Dispersal mode, seed shadows, and colonization patterns. *Vegetatio* 107/108: 261-280.
- Willson, M.F., Irvine, A.K. & Walsh, N.G. 1989. Vertebrate dispersal syndromes in some Australian and New Zealand plant communities, with geographical comparisons. *Biotropica* 21: 133-147.
- Willson, M.F., Rice, B.L. & Westoby, M. 1990. Seed dispersal spectra: a comparison of temperate communities. *J. Veg. Sci.* 1: 547-560.
- Willson, M.F., Traveset, A. 2000. The ecology of seed dispersal. Seeds: the ecology of regeneration in plant communities (ed. by M. Fenner), pp. 85-110. CABI Publishing, Wallingford.
- Wilson, D.S. 1992. Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. *Ecology* 73: 1984-2000.
- Wilson, J.B. & Anderson B.J. 2001. Species-pool relations: like a wooden light bulb. *Folia Geobot.* 36: 35-44.
- Wilson, J.B. 1992. Limitations to plant species coexistence at a point: a study in a New Zealand lawn. *J. Veg. Sci.* 3: 711-714.
- Wilson, S.D. & D. Tilman. 2002. Quadratic variation in old-field species richness along gradients of disturbance and nitrogen. *Ecology* 83: 492-504.
- Witte, J.P.M. & Torfs, P.J.J.F. 2003. Scale dependency and fractal dimension of rarity. *Ecography* 26, 60-68.
- Witte, J.P.M. 1998. National water management and the value of nature. PhD Thesis Wageningen Agricultural University.
- Wolters, M.J. & Bakker, J.P. 2002. Soil seedbank and driftline composition along a successional gradient on a temperate salt marsh. *Appl. Veg. Sci.* 5: 55-62.
- Worthington, A.H. 1989. Adaptations for avian frugivory: assimilation efficiency and gut transit time of *Manacus vitellinus* and *Pipra mentalis*. *Oecologia* 80: 381-389.
- Xiong, S., Johansson, M.E., Hughes, F.M.R. et al. 2003. Interactive effects of soil moisture, vegetation canopy, plant litter and seed addition on plant diversity in a wetland community. *J. Ecol.* 91: 976-986.
- Young, A., T. Boyle & T. Brown. 1996. The population genetic consequences of habitat fragmentation for plants. *Trends Ecol. Evol.* 11: 413-418.
- Young, T.P., D.A. Petersen & J.J. Clary. 2005. The ecology of restoration: historical links, emerging issues and unexplored realms. *Ecol. Lett.* 8: 662-673.
- Zens, M.S. & Peart, D.R. 2003. Dealing with death data: individual hazards, mortality and bias. *Trends Ecol. Evol.* 18: 366-373.
- Zobel, K. 2001. On the species-pool hypothesis and the quasi-neutral concept of plant community diversity. *Folia Geobot.* 36: 3-8.
- Zobel, M. & Kalamees 2005. Diversity and dispersal - Can the link be approached experimentally? *Folia Geobot.* 40: 3-11.
- Zobel, M. 1997. The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence. *Trend Ecol. Evol.* 12: 266-269.
- Zobel, M., Opik M., Moora M. & M. Pärtel 2006. Biodiversity and ecosystem functioning: It is time for dispersal experiments. *J. Veg. Sci.* 17: 543-547.
- Zobel, M., Van Der Maarel E. & Dupré C. 1998. Species pool: The concept, its determination and significance for community restoration. *Appl. Veg. Sci.* 1: 55-56.



Summary

Growing concern about the ongoing loss of biodiversity has resulted in increased efforts throughout the world to protect endangered species and to conserve and restore endangered ecosystems. Efficient conservation and restoration of plant diversity requires a predictive ecology based on general principles for the assembly of plant communities (so called ‘assembly rules’).

There is currently a wealth of theories on the processes that shape the species composition of local plant communities. These theories can be grouped into three broad views according to the main processes involved (Chapter 1 and 9). (1) The niche-based view asserts that local species composition is a deterministic consequence of local interactions between the extant species in a plant community and their environment, based on differences between species in terms of resource usage, stress tolerance and resistance to disturbance. (2) The dispersal-based view assigns a prominent role to dynamics of habitat patches in combination with differences between species in their ability for dispersal in space and time. (3) The trait-neutral view is based on stochastic processes in which local species composition is determined by the abundance of species in the regional species pool. These three sets of processes respectively correspond to three different factors shaping the assembly of plant communities: (1) the abundance of microsites with a suitable environment for establishment and subsequent survival (microsite limitation); (2) the degree of long-distance seed dispersal (dispersal limitation); and (3) the abundance of populations in the surrounding areas that act as seed sources (seed source limitation). At local scale, the combined effects of 2 and 3 result in a limited availability of seeds in suitable habitat patches (seed limitation). Empirical evidence for the relative importance of these three sets of processes is, however, still surprisingly limited.

Among scientific projects on the assembly of plant communities, there is a trade-off between realistic complexity and simplification. Although experiments are a prerequisite for a detailed understanding of processes involved in community assembly, these experiments typically involve small spatial and temporal scales, which makes generalizations difficult. Moreover, the experimental designs are often too artificial to represent natural systems. Generalizations across larger sets of species and ecosystems therefore require complementary approaches. This thesis explores such a complementary, statistical approach, based on the premise that the combination of large ecological databases can generate clues to the processes at work in the assembly of plant communities which are valid at larger spatial and temporal scales. We combined large databases with information on community composition (described in Chapter 1, Box 2) and on functional traits (described in Chapter 2) to compare the predictive power of the three views of community assembly. Our premise was that differences with regard to relevant functional traits

between species from local habitat patches and from the regional species pool can give clues to the processes at work in the assembly of local plant communities. The advantage of focusing on functional traits instead of species is that it simplifies raising the scale level from species to communities. The integration of vast ecological databases at different organizational levels and across spatial scales to reveal new information can be regarded as an example of the emerging field of 'ecoinformatics' (Chapter 1, Box 1).

An analysis of a large database with species composition data from vegetation plots using ordination techniques (Chapter 3) revealed that species clearly sort along environmental gradients. This implies that patterns of species composition across habitat types can be reliably predicted from a few key environmental conditions, which is consistent with the niche-based view. These environmental variables can therefore be used as predictors (filters) to assemble a list of species that are potentially able to coexist in small-scale plots within a given habitat, the so-called habitat species pool.

Despite the high predictability of the habitat species pool, Chapter 3 also revealed that at the scale of individual plots, many species are absent which might be expected to be present, given the combination of environmental conditions. The fact that the distribution of many species is characterized by the common occurrence of suitable but unoccupied habitat patches might be explained by the limited availability of seeds. This thesis describes the impact of seed limitation across several levels of organization.

In the first place, the probability of local occurrence proved to be greatly affected by the abundance of seed sources in the regional species pool, irrespective of species-specific traits (Chapter 6). There is thus a large role for stochastic, abundance-driven processes. This result is consistent with the trait-neutral view of community assembly. In effect, recruitment in suitable habitat patches takes the form of a lottery, and the chances in this recruitment lottery for a given patch are thus largely dictated by the regional abundance of species. This implies that the assembly of local plant communities has an inherent element of unpredictability when only the traits of the component species are taken into account.

In addition to these trait-neutral processes, trait-based processes are shown to be important at the level of species, communities and landscapes. At the species level there were large differences between the degree of seed limitation due to differences in life-history traits (consistent with the dispersal-based view). The ability to track suitable habitat patches was increased by a few orders of magnitude by a greater capacity for long-distance dispersal, greater adult longevity and the capacity to build a persistent seed bank (Chapter 3). On average, species with high scores for all three traits had the highest frequency of occurrence within suitable habitat patches.

Local plant communities are connected to each other by long-distance dispersal to form so-called metacommunities. At the level of metacommunities, there were differences between habitat types in the representation of dispersal traits,

due to interactive effects between niche-based processes and the efficiency of dispersal processes (Chapter 5). The resulting trait–environment patterns were much stronger at the level of plant communities than at the species level, which implies a non-random selection of species from the regional species pool with regard to their dispersal traits. The efficiency of dispersal thus depends on the environmental context. Species with high dispersal abilities prevailed in habitats with large-scale or high-intensity disturbances, while adaptations for long-distance dispersal were less common in late successional stages (Chapter 5). Moreover, in habitat types with an open vegetation structure, species that are effectively transported by multiple dispersal vectors (polychory) appeared to be the rule rather than the exception.

At the landscape level, the degree to which available seeds are actually transported is determined by the availability of dispersal vectors, which act like a complex ‘dispersal infrastructure’. The characteristics of this dispersal infrastructure can vary in space and time, and this may induce changes in local species composition. In fact, the most important finding of our research was that differences between species in their adaptations to various dispersal vectors are a key factor in explaining losses of plant diversity in Northwest Europe in the 20th century, with water- or fur-assisted dispersal being over-represented among declining species, while others (wind- or bird-assisted dispersal) are under-represented (Chapter 8). This implies that past changes in the dispersal infrastructure are at least as important in explaining diversity losses as the conventional explanation of environmental change. Present-day species losses are thus the legacy of the ‘ghost of land-use past’.

The combined results of this thesis suggest that the three sets of processes (niche-based, dispersal-based and abundance-based) can be regarded as iterative (Chapter 9). We thus expect that the three views can reinforce each other and that integrating them will increase our understanding of community assembly. To reconcile the three views of community assembly, it may be fruitful to search for relationships between traits that equip species for local survival versus dispersal traits. Chapter 4 provides empirical evidence for the existence of a ‘persistence – dispersal trade-off’ across a large set of plant species, although this trade-off appears to be weak and complicated (see Chapter 4 for further discussion). Even if the trade-off is weak, it implies that at regional scale, low dispersal abilities can probably be counterbalanced to some degree by a higher local aboveground persistence, i.e. higher competitive abilities or higher stress tolerance, leading to lower rates of local aboveground extinction. If trade-offs between functional traits lead to an equalization of variation in fitness across species (i.e. species having the same chance to be present in the next generation) this might in fact be the ultimate reason why the trait-neutral view of community assembly performs so surprisingly well in describing patterns of relative abundance of species within and across communities. Trade-offs may therefore provide a clue for ways to reconcile trait-based and trait-neutral views of community assembly (Chapter 9).

The results reported in Chapter 4 also revealed that many species have a half-life expectation far exceeding 15 years, which may contribute to considerable time lags after changes in habitat quality or configuration. This so-called 'extinction debt' implies the potential pitfall of underestimating the real threat status of many plant species. This underestimation of extinction risks will be most pronounced in habitats with a low nutrient availability and for immobile, perennial species with high abilities for clonal extension (Chapter 4). Apart from the extinction debt, there is also a considerable time delay in re-colonization after ecological restoration. This 'colonization deficit' will be greatest for immobile species and for species that are rare in the regional species pool (Chapters 3 and 6). At regional scale, it is thus a relatively small number of mobile species that dominate fragmented landscapes by their large numbers of individuals, while less frequent immobile species make up the majority of species and thus determine biodiversity, with ever steeper species–abundance relationships.

The ultimate consequence of the colonization deficit is that in fragmented and dynamic landscapes, it is nearly impossible to restore community types for which the targets with regard to species composition are based on historical references. This also implies a strong message for land-use policy, as it means that the creation of new habitat patches, although useful, does not offset losses of slowly colonizing species and is thus insufficient to halt diversity losses (Chapter 10). Our results indicate that the ability of species to track suitable habitat patches can be influenced in two distinct and complementary ways. The first approach involves increasing the relative abundance of immobile species in the seed rain within a given landscape (cf. Chapter 6). The second approach involves increasing the transport of available seeds by restoring dispersal processes at the landscape scale (cf. Chapter 8). Both options are discussed in Chapter 10.

Traditionally managers of nature areas focus to a large extent on influencing local environmental conditions, and they are financed accordingly in Europe. However, management measures resulting from this approach, like grazing and mowing, may also prevent the production of ripe seeds and hence greatly reduce the abundance of many immobile grassland species in the seed rain. It is suggested that this dilemma between niche-based management and dispersal-based management can be reconciled by allowing periodic, small-scale release from intensive management. With regard to seed dispersal, germination and establishment, it is not so much the mean values of management regimes that are of importance, but the variations around these mean values.

It has been proposed to create large ecological networks of nature reserves, such as the EU's prestigious and costly 'Natura 2000' framework and the 'Pan-European Ecological Network', as a tool to mitigate the effects of habitat fragmentation and to enhance the rate of dispersal between habitat patches. Although these ecological networks are mainly designed for the dispersal of large animal species, they are also expected to function as corridors for plants. There have, however, been surprisingly few empirical studies of the effectiveness of ecological

corridors for the dispersal of plant species. In fact, our findings suggest that the creation of static networks as such is probably not sufficient to halt the loss of plant diversity. Since human-induced changes in the dispersal infrastructure were shown to be one of the main drivers of species losses in Northwest Europe (Chapter 8), our findings call for restoration measures that aim to restore the dispersal infrastructure and that go beyond current conservation practices (Chapter 10). It is suggested that, although ‘naturalistic grazing’ in nature reserves, in combination with the creation of ‘robust ecological networks’ between these reserves, can be a valuable management option, this is only effective in regions that still harbour very large nature reserves. This stresses the importance of complementary approaches such as reinforcement of pastoral livestock systems, including herded and / or free-ranging livestock on common grounds (Chapter 10). The challenge will be to develop new varieties of low-input, pastoral farming systems that meet modern criteria for biodiversity and socioeconomic sustainability.

In conclusion, our research has shown that in fragmenting landscapes, dispersal is an underrated key process in explaining plant biodiversity losses, and there is an urgent need to face the consequences of this conclusion by designing a different, efficient and cost-effective form of nature conservation for the twenty-first century.



Samenvatting

HET PROEFSCHRIFT IN EEN NOTENDOP

Voor efficiënter natuurbeheer is inzicht nodig in de factoren die de mate van succes van beheer- en herstelprojecten bepalen. Een realistische inschatting van de ontwikkelingsmogelijkheden van de vegetatie is niet alleen van belang voor het behouden en ontwikkelen van natuurwaarden, maar ook voor het verkrijgen van voldoende maatschappelijk draagvlak.

Voor veel plantensoorten zijn geschikte leefgebieden beperkt tot kleine eilandjes in een zee van ongeschikte gebieden. Uit dit proefschrift blijkt dat de regionale overleving van planten in dergelijke versnipperde landschappen niet alleen afhankelijk is van de milieukwaliteit van de resterende leefgebieden, maar vooral ook van de mate waarin leeggevallen plekken weer opnieuw via zaden gekoloniseerd kunnen worden.

In tegenstelling tot grotere dieren zijn planten voor het transport van hun zaden (zaaddispersie) afhankelijk van externe vectoren, zoals wind, water, vogels en de vacht of mest van zoogdieren. Deze vectoren vormen in het landschap een complexe 'dispersie-infrastructuur' voor zaden. Het blijkt dat veranderingen in de dispersie-infrastructuur een sleutel vormen tot het verklaren van veranderingen in de Nederlandse flora in de 20^e eeuw. Veel soorten die voor hun zaadtransport afhankelijk zijn van water of de vacht van grote zoogdieren zijn sterk achteruitgegaan.

De versnippering van leefgebieden in combinatie met sterke verarming van de dispersie-infrastructuur kan leiden tot nivellering van plantendiversiteit, waarbij kritische planten geleidelijk het veld ruimen ten gunste van soorten met een meer opportunistische dispersiestrategie. De ernst van dit probleem kan gemakkelijk onderschat worden doordat veel van deze vaak langzaam reagerende planten maar heel geleidelijk uit het landschap verdwijnen. De huidige verspreidingspatronen worden dus mede bepaald door een naijleffect van vroegere vormen van landgebruik. Omgekeerd is ook de snelheid van kolonisatie van nieuwe gebieden voor veel soorten zeer beperkt.

Het huidige natuurbeleid is niet voldoende toegesneden om de vervlakking van de plantendiversiteit in Nederland tegen te gaan. Dit vraagt een andere invulling en mogelijk ook uitbreiding van de ecologische hoofdstructuur met een meer mobiele dispersie-infrastructuur voor zaden. Versterking van

de dispersie-infrastructuur in het agrarische gebied kan het ecologisch rendement van natuurgebieden en verbindingszones vergroten. Bij het verlies aan plantendiversiteit heeft de landbouw een belangrijke rol gepeeld, maar paradoxaal genoeg ligt de sleutel tot het succes van behoud en herstel van plantendiversiteit ook voor een deel bij de landbouw.

Achtergrond: tegenvallende resultaten bij herstelbeheer

Wereldwijd staat de biologische diversiteit (biodiversiteit) onder druk. Het keren van deze trend blijkt in de praktijk een lastige opgave. Naast sociaal-economische knelpunten vormt een gebrek aan kennis over de achterliggende processen een belangrijke beperking voor het efficiënt behouden en herstellen van de biologische rijkdommen. De Nederlandse Organisatie voor Wetenschappelijk Onderzoek (NWO) levert via het Stimuleringsprogramma Biodiversiteit een bijdrage aan de vermeerdering van kennis over biodiversiteit. Dit promotieonderzoek vormt een klein onderdeel van dat grote geheel en richt zich op vaatplanten en de vegetatie die ze samen vormen (plantengemeenschappen).

Veranderingen in de mate van voorkomen van planten in Noordwest-Europese landschappen kunnen voor een belangrijk deel verklaard worden door het verdwijnen van leefgebieden (habitats) van soorten en door veranderingen in de kwaliteit van de overgebleven leefgebieden als gevolg van de effecten van vermessing, verzuring en verdroging. Vooral vermessing ligt als een soort nivellerende deken over het landschap, waarbij een beperkt aantal snelgroeiende en concurrentiekrachtige plantensoorten profiteert ten koste van langzamer groeiende soorten (hoofdstuk 1 en 8).

Het natuurbeleid in Nederland heeft zich de laatste decennia steeds offensiever opgesteld en steekt veel energie in het omvormen van gedegeneerde en soortenarme ecosystemen naar halfnatuurlijke ecosystemen die plaats bieden aan een hogere diversiteit aan planten en dieren. Uitgangspunt hierbij is dat het herstel van geschikte milieucondities op een bepaalde plek automatisch leidt tot een snelle (her)vestiging van kenmerkende plantensoorten.

Herstelbeheer heeft in Nederland tot nu toe een reeks opmerkelijke successen gekend, waarbij zich in korte tijd fraaie plantengemeenschappen ontwikkelden met vele bedreigde plantensoorten. Bij een aanzienlijk deel van de projecten vallen de resultaten echter tegen doordat veel bedreigde soorten die verwacht worden op basis van de herstellende milieucondities, zich niet (her)vestigen. Het omgekeerde komt trouwens ook regelmatig voor: de vestiging van bedreigde soorten die juist niet verwacht werden. Kortom: voor een efficiënter natuurbeheer is inzicht nodig in de factoren die de vegetatieontwikkeling van dergelijke herstelprojecten sturen. Een realistische inschatting van de ontwikkelingsmogelijkheden in een bepaald gebied is niet alleen van belang voor het beschermen en ontwikkelen

van natuurwaarden, maar ook voor het behoud en creëren van voldoende maatschappelijk draagvlak. Meer in het algemeen is de centrale vraag in dit proefschrift: welke factoren bepalen de soortensamenstelling van lokale plantengemeenschappen.

Drie groepen processen als filters op de soortensamenstelling van plantengemeenschappen

De plantensoorten die samen voorkomen op een bepaalde habitatplek (lokale plantengemeenschap) zijn slechts een subset van de soorten die in het omringende landschap in het desbetreffende habitattype voorkomen (de soortenpool). De processen die het verschil bepalen, kunnen beschouwd worden als een soort filters op deze soortenpool. Het is daarbij nuttig om niet alleen te kijken naar individuele soorten, maar ook naar de eigenschappen die hun functioneren beïnvloeden (Engels: functional traits). Een belangrijk uitgangspunt in dit onderzoek is dat verschillen in het spectrum aan functionele eigenschappen (Engels: trait values of attributes) tussen de lokale plantengemeenschap en de soortenpool in de omgeving informatie geeft over de achterliggende processen. De filters werken namelijk niet op naamplaatjes van soorten, maar op hun functionele eigenschappen. Het is vervolgens de uitdaging voor ecologen om de belangrijkste filters en de relevante eigenschappen te kwantificeren.

Er zijn vele theorieën over de processen die een rol spelen bij het bepalen van de soortensamenstelling van lokale plantengemeenschappen. Deze theorieën kunnen ruwweg in drie groepen verdeeld worden aan de hand van de beperkende factoren: (1) Er zijn te weinig geschikte plekken voor de kieming van zaden en de aansluitende (her)vestiging van een lokale populatie, (2) er is te weinig transport van zaden vanuit populaties in de omgeving, (3) er zijn te weinig zaadbronnen aanwezig in de omgeving. In het eerste geval is de kwaliteit van de habitatplek zelf de beperkende factor terwijl in het tweede en derde geval de beschikbaarheid van zaden voor kolonisatie van de habitatplek het knelpunt vormt. Bij de tweede visie spelen verschillen tussen soorten in hun dispersiecapaciteit de hoofdrol, terwijl bij de derde visie toevalsprocessen de sturende factor zijn. Het is niet goed bekend wat het relatieve belang is van deze drie factoren en door welke condities dit bepaald wordt. Dit onderscheid is echter van belang voor het beleid en beheer, aangezien het oplossen van de verschillende knelpunten andere strategieën vergt.

Van metapopulatie naar metacommunity

In dit promotieproject is gekeken naar het relatieve belang van zaadtransport (zaaddispersie) bij het verklaren van de soortensamenstelling van lokale plantengemeenschappen. Hier wordt gemakshalve gesproken over zaden, maar in feite gaat het om diasporen, dat wil zeggen alle plantdelen die na transport kunnen leiden tot een nieuw individu, inclusief niet-seksuele plantdelen die als stekjes fungeren. In tegenstelling tot grotere dieren zijn planten voor het transport van hun zaden afhankelijk van externe vectoren, zoals wind, water, vogels en de vacht of

mest van zoogdieren. Deze dispersievectoren vormen gezamenlijk in het landschap een complexe ‘*dispersie-infrastructuur*’.

De lokale plantengemeenschappen vormen vaak eilandjes van een bepaald habitatype (leefgebied) temidden van een zee van andere habitattypen. De lokale populaties in deze habitatplekken kunnen met elkaar in verbinding staan door de uitwisseling van zaden (en daarmee ook genen). Als er voldoende zaadtransport tussen de deelpopulaties is, dan vormen de subpopulaties gezamenlijk een metapopulatie. De mate van voorkomen van een plantensoort in een dergelijke metapopulatie hangt af van de dynamische balans tussen de mate waarin zaden geschikte habitatplekken kunnen koloniseren en de mate waarin lokale populaties verdwijnen (lokale extinctie).

Doordat mensen steeds meer ruimte in beslag nemen, is de mate van isolatie tussen habitatplekken in grote delen van de wereld sterk toegenomen. Dit verschijnsel wordt habitatversnippering genoemd. De mate van versnippering van een landschap heeft waarschijnlijk een sterk effect op de mate van zaadtransport. Daarnaast is ook de beschikbaarheid en diversiteit van dispersievectoren voor zaden in de 20e eeuw sterk veranderd (hoofdstuk 8, box 3). Beide processen kunnen leiden tot veranderingen in de soortensamenstelling van lokale plantengemeenschappen. Veel onderzoek aan zaaddispersie van planten richt zich echter op een of enkele soorten en er is nog weinig bekend over het relatieve effect van dispersieprocessen op de soortensamenstelling van gehele plantengemeenschappen. Dit vergt een uitbreiding van de metapopulatie benadering waarin elke soort apart wordt bekeken, naar een metacommunity benadering waarin de lokale plantengemeenschappen in hun onderlinge samenhang in het landschap bestudeerd worden (hoofdstuk 1, figuur 1.3). Om de effecten van habitatversnippering tegen te gaan is gedetailleerde kennis nodig over het achterliggende complex van processen. De resultaten van dit onderzoek leveren hieraan een bijdrage.

Een nieuwe benadering met eco-informatica

Bij ecologisch onderzoek is er een dilemma tussen de precisie waarmee dingen worden geanalyseerd en de mate waarin de resultaten gegeneraliseerd kunnen worden. Voor het ontrafelen van de processen die de soortensamenstelling van plantengemeenschappen bepalen zijn laboratorium- en veldexperimenten onontbeerlijk. De ruimtelijke en temporele schaal van zulke experimenten zijn echter beperkt. Sommige processen, waaronder zaadtransport over grote afstanden, zijn toevalsafhankelijk en moeilijk meetbaar in kortlopende experimenten. Er is daarom behoefte aan een aanvullende benadering die generalisaties mogelijk maakt voor grote sets aan soorten en ecosystemen.

In dit project is gekozen voor een complementaire benadering op basis van het integreren en analyseren van twee grote ecologische databases. In de eerste plaats de Landelijke Vegetatie Databank, waarin ruim 480.000 beschrijvingen bijeengebracht zijn van de soortensamenstelling in kleine plots (hoofdstuk 1, box 2). Deze zogenaamde vegetatieopnamen kunnen beschouwd worden als een steekproef

van de lokale plantengemeenschap zoals die voorkomt op een habitatplek. Daarnaast is er een database opgebouwd voor de Nederlandse flora met daarin informatie over het vermogen van hun zaden (diasporen) voor transport over lange afstanden (hoofdstuk 2). Hierbij is soortspecifieke informatie opgenomen over de volgende dispersievectoren met een hoge potentie voor lange-afstand transport: wind, water, vogels en de vacht of mest van grote zoogdieren. Ook is informatie opgenomen over het vermogen om als zaad in de bodem te overleven en zo een ondergrondse zaadvoorraad op te bouwen.

Een dergelijke benadering, waarbij nieuwe informatie wordt verkregen met behulp van de integratie en analyse van ecologische databases van verschillende organisatieniveaus, vormt onderdeel van het nieuwe werkgebied van de eco-informatica. De aanwezige ruimtelijk variatie in omgevingsfactoren en veranderingen in landgebruik kunnen dan beschouwd worden als een grootschalig 'natuurlijk experiment'.

In box 1 worden meer achtergronden gegeven van deze nieuwe eco-informatica benadering. Verder wordt in hoofdstuk 6 een methode beschreven voor de analyse van de verschillende soortenpools en de filters die het verschil in soortensamenstelling tussen deze soortenpools bepalen. Globaal kunnen hierbij twee typen filters onderscheiden worden. In de eerste plaats kunnen milieucondities beschouwd worden als een serie filters die per habitat een set soorten met bepaalde eigenschappen doorlaten (de zogenaamde habitat soortenpool). Het tweede type filter is gebaseerd op de mate van aanvoer van zaden vanuit de bodem (kieming uit de zaadvoorraad) en vanuit de omgeving (zaadregen). Het aanbod aan bronpopulaties voor zaden in een bepaald gebied kan beschouwd worden als de geografische soorten pool. Deze geografische subset van de totale soortenpool kan op verschillende ruimtelijke en temporele schaalniveaus gekwantificeerd worden.

Hoe voorspelbaar is het voorkomen van planten op basis van milieucondities?

Het natuurbeheer in Nederland is gebaseerd op de aanname dat de soortensamenstelling van lokale plantengemeenschappen min of meer in evenwicht is met de heersende milieucondities. Uit hoofdstuk 3 blijkt dat de set soorten die in een bepaald habitattypen kan groeien (de habitat soortenpool) goed te voorspellen is op basis van de lokale milieuomstandigheden in combinatie met kennis van de ecologische niche van soorten. De drie belangrijkste milieufilters voor binnenlandse vegetaties in Nederland zijn: vochtgehalte van de bodem, beschikbaarheid van nutriënten (gecorrleerd met pH) en beschikbaarheid van licht. Daarentegen is de voorspelbaarheid van de daadwerkelijk gerealiseerde lokale soortensamenstelling zeer laag (meer dan 90% onverklaarde variatie). Veel plantensoorten laten habitatplekken onbezet terwijl deze qua milieu wel geschikt lijken. Dit duidt erop dat vermoedelijk ook andere processen een rol spelen zoals de beperkte beschikbaarheid van zaden. In dit proefschrift wordt aangetoond dat de mate waarin planten geschikte habitatplekken bezetten inderdaad voor een groot deel afhangt van de beschikbaarheid van zaadbronnen en van de dispersiecapaciteit van de soorten.

De grote rol van stochastische processen: kolonisatie als gewogen loterij

De kans dat een geschikte habitatplek bezet wordt door een bepaalde plantensoort, blijkt in de eerste plaats af te hangen van de frequentie van voorkomen van de soort in de regionale soortenpool (hoofdstuk 6). Dit effect kan verklaard worden door stochastische processen (afhankelijk van het toeval): hoe meer zaadproducerende populaties van een soort er in de metapopulatie voorkomen, hoe groter de kans dat zaden onbezette gebieden koloniseren. Hierdoor verschuift de dynamische balans tussen kolonisatie en lokale extinctie in het voordeel van de eerste component. Doordat het transport van zaden over grote afstanden een relatief zeldzaam toevalsproces is, kan de kolonisatie van geschikte habitatplekken beschouwd worden als een loterij. Hoofdstuk 6 laat zien dat de kansen van een soort in een bepaald gebied in de eerste plaats worden bepaald door de hoeveelheid effectieve zaadbronnen in de omgeving, een gewogen loterij dus. Voor veel plantensoorten zijn bezette leefgebieden teruggedrongen tot kleine eilandjes van ecologisch kapitaal temidden van een zee van menselijk kapitaal. Bij een dergelijke sterke versnippering zijn de kansen in de loterij dus bijzonder gering.

Het omgekeerde geldt echter ook: als de zaadtoevoer maar groot genoeg is, dan kunnen sommige soorten zich prima vestigen en handhaven in habitatplekken met een marginale kwaliteit. Dit betekent ook dat verschuivingen in de regionale soortenpool, bijvoorbeeld onder invloed van een veranderend landgebruik, op termijn kunnen leiden tot nieuwe allianties van soorten ('emerging ecosystems'), zelfs als de milieucondities gelijk blijven. Doordat de regionale soortenpool in de 20^e eeuw sterk is veranderd, is het dus onmogelijk om lokale plantengemeenschappen in al zijn details te restaureren gebaseerd op historische referenties. Verschuivingen in de regionale soortenpool onder invloed van klimaatverandering zullen dit effect nog verder versterken.

De grote rol van stochastische processen wil echter niet zeggen dat meer deterministische processen, gebaseerd op de eigenschappen van soorten, er niet toe doen. Uit dit proefschrift komt de rol van dispersiekenmerken duidelijk naar voren op drie niveaus: soort, ecosysteem en landschap.

Soortniveau: langzame plantensoorten in dynamische landschappen

De mate waarin planten geschikte habitatplekken kunnen bereiken hangt af van soorteigenschappen die de mobiliteit van planten beïnvloeden (hoofdstuk 3). De mate waarin geschikte habitatplekken ook daadwerkelijk bezet zijn is groter voor soorten met een hoge dispersiecapaciteit, voor soorten die bovengronds lang overleven en voor soorten met een lang levende zaadvoorraad in de bodem. Het voorkomen van soorten die op alle drie de kenmerken hoog scoren, zoals Grote lisdodde (*Typha latifolia*), is daardoor relatief goed voorspelbaar. Aan de andere kant laten soorten die op deze drie kenmerken laag scoren, zoals Heidekartelblad (*Pedicularis sylvatica*), veel habitatplekken onbezet. Het is jammer voor het natuurbeleid dat juist veel bedreigde soorten laag scoren op dispersiecapaciteit

(hoofdstuk 3). In landschappen waarin de levensduur van habitatplekken afneemt door veranderend landgebruik of door klimaatveranderingen zullen deze planten steeds meer habitatplekken onbezet laten. Deze planten gebruiken de beschikbare habitatplekken dus op een inefficiënte wijze en dit zal waarschijnlijk leiden tot een achteruitgang van 'langzame planten' in dynamische landschappen. De populatiedynamiek loopt als het ware uit de pas met de landschapsdynamiek.

Zelfs bij soorten die speciale aanpassingen hebben voor zaadtransport via de wind (zoals zaden met een parachute van een krans geveerde haren), blijkt dat de kans op dispersie over afstanden meer dan 100 meter zeer klein is. Uit modelberekeningen voor 190 soorten hogere planten (hoofdstuk 7) blijkt dat er slechts enkele soorten zijn waarbij meer dan 1 procent van de zaden een afstand van meer dan een kilometer aflegt: Wilgenroosje (*Chamerion angustifolium*), Riet (*Phragmites australis*) en Grote lisdodde (*Typha angustifolia*). Voor diverse bedreigde soorten met aanpassingen aan zaaddispersie door wind ligt de afstand die de verste 1 procent van de zaden overbruggen ver onder de 100m, zoals bij Valkruid (*Arnica montana*) en Spaanse ruiter (*Cirsium dissectum*). Het blijkt dat de regionale overleving van planten sterker beïnvloed wordt door de extreme afstanden die afgelegd worden door 1 procent van de zaden dan door de mediane dispersieafstand. De zeldzame uitzonderingsgevallen hebben bij zaadverspreiding op de lange duur meer effect dan het gemiddelde.

Samenvattend kan worden gesteld dat bij veel planten de zaden in de versnipperde Nederlandse landschappen te dicht bij de ouderplant vallen om bij te kunnen dragen aan een effectieve kolonisatie van nieuwe gebieden. Voor het natuurbeleid betekent dit dat de mate van lokale realisatie van natuurdoeltypen op basis van alleen milieufactoren slecht voorspeld kan worden.

Ecosysteemniveau: interacties tussen milieu en dispersie

Dispersiestrategieën laat een duidelijke relatie zien met de drie belangrijkste milieugradiënten en dan vooral met de beschikbaarheid van licht (hoofdstuk 5). Bij veel dispersievectoren komen soorten met een hoge dispersiecapaciteit vooral voor in open begroeiingen met veel dynamiek door grootschalige en/of frequente verstoringen. Deze patronen zijn sterker op het niveau van ecosystemen dan op het niveau van soorten, zodat de efficiëntie van dispersie blijkbaar beïnvloed wordt door lokale milieuomstandigheden. Er is dus een interactie tussen abiotische (niche-gerelateerde) processen en dispersieprocessen.

Habitattypen herbergen vaak maar enkele plantensoorten die in veel habitatplekken voorkomen (kernsoorten), terwijl de grote meerderheid van de soorten op een gering aantal habitatplekken voorkomt (satellietsoorten; figuur 1.2). Zeldzaamheid is dus een algemeen verschijnsel. Uit hoofdstuk 9 blijkt dat veel kernsoorten gekenmerkt worden door een potentie om via meerdere dispersievectoren getransporteerd te worden (polychory). In open, dynamische vegetatie is polychory eerder regel dan uitzondering. In oudere, meer gesloten successiestadia, zoals bossen, is er echter geen verschil in het aantal potentiële dispersievector-

ren tussen kernsoorten en satellietsoorten. Hier spelen blijkbaar andere factoren een rol bij het bepalen van de frequentie van voorkomen.

Een ander opmerkelijk resultaat is dat water als transportmechanisme voor zaden niet alleen belangrijk is in water- en oevervegetatie. Ook in slechts incidenteel overstroomde begroeiingen komen relatief veel soorten met drijvende zaden voor (20-30%, hoofdstuk 5). Dit betekent dat overstromingen van zulke begroeiingen, ondanks de lage frequentie, van grote betekenis kan zijn voor het transport van zaden.

Een praktisch gevolg van de verschillen in het spectrum aan dispersiekenmerken tussen habitattypen is dat de habitattypen onderling verschillen in hun gevoeligheid voor habitatfragmentatie en in de potenties voor herstel. Deze potenties zijn bijvoorbeeld relatief hoog in rietgemeenschappen, knopbiesvegetatie en overstromingsgraslanden, terwijl ze relatief laag zijn in eiken-haagbeukenbos en droge kalkrijke duingraslanden (hoofdstuk 5).

Landschapsniveau: de dispersie-infrastructuur

De mate waarin de beschikbare zaden ook daadwerkelijk getransporteerd worden is afhankelijk van de beschikbaarheid van dispersievector(en) (m.n. wind, water, grote zoogdieren, vogels, verkeer) in een landschap. Deze vectoren vormen gezamenlijk een complexe dispersie-infrastructuur voor zaden. In de 19^e en 20^e eeuw is de diversiteit in de dispersie-infrastructuur sterk verarmd en in veel landschappen zijn water en grote zoogdieren geheel weggefallen als transportvector. Ook als de vectoren nog wel aanwezig zijn in het landschap is de uitwisseling tussen habitatplekken vaak verdwenen. In rivier- en beekdalen stonden in het verleden veel gebieden met elkaar in contact via oppervlaktewater als gevolg van natuurlijke overstromingen en kunstmatige bevoeiing. Ook de bewegingsruimte voor grote zoogdieren (vee) was groot via een uitgebreid netwerk van veedriften en het gebruik van gemeenschappelijke weidegronden. Hierdoor stonden niet alleen graslanden met elkaar in contact maar ook vele andere habitattypes die langs de route door de dieren bezocht werden (zie hoofdstuk 8, box 3). Hier tegenover staat dat sommige soorten er nieuwe transportvectoren bij gekregen hebben in de vorm van menselijk gesleep (o.a. met grond) en verkeer (hechting van zaden aan banden en schoeisel).

Een belangrijk resultaat van dit onderzoeksproject is dat veranderingen in de dispersie-infrastructuur een sleutel vormen tot het verklaren van veranderingen in de Nederlandse flora in de 20^e eeuw (hoofdstuk 8). Het effect hiervan ligt in dezelfde orde van grootte als het welbekende effect van vermesting. In het bijzonder veel soorten die voor hun zaadtransport afhankelijk zijn van water of de vacht van grote zoogdieren zijn in de 20^e eeuw sterk achteruitgegaan. Soorten die zich verbreiden via wind of vogels doen het over het algemeen juist relatief goed. Verder leidt het vermogen om een langlevende zaadvoorraad in de bodem te vormen tot een aanzienlijke vermindering van het risico op lokaal uitsterven. Dit bufferende effect van een zaadvoorraad is waargenomen bij alle dispersievectoren.

Dilemma tussen dispersie en lokale overleving

De gecombineerde resultaten van dit proefschrift suggereren dat de drie sets van processen (gebaseerd op niches, zaaddispersie en frequentie in de regionale soortentpool) beschouwd kunnen worden als iteratief (hoofdstuk 9). Dispersieprocessen beïnvloeden daardoor niet alleen de soortensamenstelling, maar waarschijnlijk ook (indirect) het functioneren van ecosystemen. Het valt dan ook te verwachten dat een integratie van de drie sets aan processen ons begrip van de opbouw (Engels: assembly) van plantengemeenschappen vergroot.

Voor een integratie van de drie sets van processen is gezocht naar relaties tussen kenmerken die van belang zijn voor de bovengrondse overleving en die van belang zijn voor het koloniseren van habitatplekken. Deze kenmerken kunnen met elkaar verbonden zijn doordat een investering in het ene kenmerk ten koste gaat van de mogelijkheden om te investeren in een ander kenmerk. Een dergelijk dilemma tussen twee functies die een plant niet tegelijkertijd kan optimaliseren wordt in het Engels trade-off genoemd. Dergelijke trade-offs reduceren het spectrum aan mogelijke combinaties van eigenschappen (trait values) en een beter begrip hiervan helpt bij het aggregeren van soorten in functionele groepen of strategieën.

In hoofdstuk 4 worden inderdaad aanwijzingen gevonden dat een beperkt vermogen voor zaaddispersie in ruimte of tijd tot op zekere hoogte gecompenseerd wordt door een langere levensduur van de volwassen plant. Met behulp van 845 proefvlakken waarin de soortensamenstelling elk jaar gedurende 5 tot 40 jaar is genoteerd, is voor 276 plantensoorten (excl. bomen en stuiken) een overlevingscurve berekend. Een groot deel van de meerjarige soorten blijkt een levensverwachting (half-life expectation: T_{50}) te hebben van meer dan 15 jaar. Het blijkt dat soorten die als volwassen plant bovengronds lang overleven, over het algemeen een korter levende zaadvoorraad in de bodem hebben en een beperkter vermogen om hun zaden via wind te transporteren. Deze negatieve relatie is echter gecompliceerd en niet erg sterk. Er zijn daardoor diverse uitzonderingen van planten die 'ontsnappen' aan de trade-off door een lange bovengrondse overleving te combineren met een hoge dispersiecapaciteit.

Vertragingseffecten bij uitsterven en kolonisatie

De lange bovengrondse overleving van veel plantensoorten, zoals hierboven beschreven, kan bijdragen aan een sterke vertraging van het lokaal uitsterven van subpopulaties. Dit geldt vooral voor planten die zich lokaal uitbreiden via langlevende clonale connecties tussen de ouderplant en het nageslacht en voor plantensoorten van nutriëntenarme bodems (hoofdstuk 4). Dit vertragingseffect leidt ertoe dat het effect van habitatversnippering en een verarming van de dispersie-infrastructuur pas na verloop van tijd in volle omvang duidelijk wordt. In het Engels wordt dit 'extinction debt' genoemd (een soort 'uitsterf schuld' van onze generatie voor de toekomst).

De huidige verspreidingspatronen worden dus bepaald door een naijleffect van vroegere vormen van landgebruik. De valkuil voor het natuurbeleid is dat het lan-

gere termijn perspectief voor de overleving van langzame planten die afhankelijk zijn van verdwenen dispersievectoren hierdoor te rooskleurig ingeschat wordt. Doordat veel van deze langlevende soorten ook een beperkte dispersiecapaciteit hebben (hoofdstuk 4), is ook omgekeerd de snelheid van (her)kolonisatie van nieuwe gebieden voor veel van deze soorten beperkt.

Perspectieven voor beleid en beheer

Dit proefschrift maakt duidelijk dat de combinatie van habitatversnippering met een sterke verarming van de dispersie-infrastructuur een sleutelfactor vormt voor veranderingen in de Noordwest-Europese flora. Dit kan in veel landschappen leiden tot een vervlakking van plantendiversiteit, waarbij weinig mobiele planten en soorten die hun belangrijkste dispersievector verloren hebben, geleidelijk aan het veld ruimen ten gunste van soorten met een meer opportunistische dispersiestrategie (hoofdstuk 8). De sleutel voor het keren van deze trend ligt bij het herstellen van dispersieprocessen op landschapsschaal.

Vanuit het natuurbeheer zijn er ruwweg twee aangrijpingspunten om de mate van zaadtransport van weinig mobiele soorten te vergroten. In de eerste plaats het vergroten van het relatieve aandeel van zaden in de zaadregen zodat de kansen in de gewogen loterij toenemen, en in de tweede plaats het restaureren van de dispersie-infrastructuur. Voor beide opties worden hieronder enkele suggesties gedaan (voor details zie hoofdstuk 10).

Verhogen rendement van het ecologisch geheugen

De resultaten van dit onderzoek suggereren dat het rendement van herstelmaatregelen voor de vegetatie laag is wanneer de beschikbaarheid van zaden van weinig mobiele soorten gering is in zowel de ondergrondse zaadvoorraad als in de zaadregen vanuit de omgeving. Het rendement van het creëren van nieuwe habitatplekken kan verhoogd worden door bij de ruimtelijke planning van inrichting- en herstelprojecten zo veel mogelijk aan te sluiten bij de nog aanwezige populaties. Buiten de bestaande natuurgebieden komen in veel agrarische landschappen nog steeds restanten voor van oude landschapselementen, zoals houtwallen, singels en slootkanten met daarin 'relictpopulaties' van weinig mobiele soorten. Zeker in gebieden met een verarmde soortenpool kunnen deze relictpopulaties dienen als belangrijke zaadbronnen. De in het landschap nog beschikbare relictpopulaties kunnen dan beschouwd worden als een soort '*extern ecologisch geheugen*' van waaruit onbezette leefgebieden gekoloniseerd kunnen worden. Het vertragingseffect bij lokaal uitsterven kan hierbij dus in ons voordeel werken, mits we niet te lang wachten. In plaats van een valkuil voor het beleid kunnen we dit vertragingseffect dus gebruiken als een soort verzekering voor de toekomst.

Ook in het gebied zelf kan de vegetatiehistorie een bruikbare erfenis nalaten voor het natuurbeheer in de vorm van een zaadvoorraad. Deze ondergrondse potenties kunnen beschouwd worden als een '*intern ecologisch geheugen*'. Het stimuleren van kieming van zeldzame soorten uit de zaadbank via de juiste vorm van

kleinschalige bodemverstoring vergt maatwerk van beheerders. De bruikbaarheid van deze methode is echter beperkt tot de deelset van soorten met langlevende zaden. Bovendien is in gebieden die intensief en langdurig agrarisch gebruikt zijn de zaadvoorraad van doelsoorten dikwijls al uitgeput. Hier kan stimulering van de zaadvoorraad, bijvoorbeeld via ontgroning of begrazing, leiden tot dominantie van een beperkte groep concurrentiekrachtige soorten, zoals Pitrus (*Juncus effusus*), Ridderzuring (*Rumex obtusifolius*) en Liesgras (*Glyceria maxima*).

Het beheer van bestaande natuurgebieden vraagt ook om aanpassingen. Grootschalige beheermaatregelen die gericht zijn op het openhouden van het landschap of op het tegengaan van de effecten van vermessing (plaggen, maaien en begrazing) laten vaak weinig ruimte voor de productie van voldoende rijpe zaden. Er is daardoor in veel terreinen een dilemma tussen beheer dat optimaal is voor de gewenste milieucondities en een beheer dat optimaal is voor het transport van zaden. Om het rendement van zaadbronnen te vergroten is het dus nodig om meer ruimtelijke en temporele variatie toe te staan in het beheerregime. Zowel voor zaaddispersie als voor kieming geldt waarschijnlijk dat niet het gemiddelde ecologisch interessant is, maar de variatie rondom dit gemiddelde.

Begrazing kan hier als een voorbeeld dienen. Zelfs bij extensieve begrazing worden van veel eetbare planten de knoppen en bloemen opgegeten nog voor ze rijp zaad kunnen produceren. Dergelijke planten kunnen een uitwijkplaats vinden in de luwte van slecht eetbare soorten in zoomvegetatie, dat wil zeggen in bloemrijke zomerruigten die deels in de winter alsnog opgegeten worden (zie figuur 10.2). Voorwaarde voor het ontstaan van zoomgemeenschappen is de aanwezigheid van voldoende ruimtelijke en temporele variatie in de graasdruk. In zeer grote gebieden kan deze variatie ontstaan via een meer natuurlijk begrazingsregime waarbij de aantallen grazers niet door mensen gereguleerd worden. Dit betekent dus geen afschot in jaren met tijdelijk zeer hoge aantallen (wat gunstig is voor het open houden van de vegetatie en het creëren van kiemingsmilieus). Maar het betekent ook dat niet bijgevoerd wordt tijdens strenge winters (dit reduceert periodiek de graasdruk in de zomer, wat gunstig is voor zaadtransport van smakelijke planten). Grote natuurgebieden met ruimte voor natuurlijke dynamiek kunnen waarschijnlijk bijdragen aan het verhogen van het rendement van zaadverspreiding van weinig mobiele plantensoorten. In Noordwest-Europa zijn veel natuurgebieden hiervoor echter simpelweg te klein. Hier zullen de beheerders dus zelf moeten zorgen voor pieken en vooral dalen in de graasdruk om zo voldoende zaadtransport van smakelijke soorten te bewerkstelligen. Dit is bovendien ook gunstig voor veel diergroepen.

Restoratie van de dispersie-infrastructuur

Het Nederlandse en Europese natuurbeleid probeert, via de aanleg van ecologische verbindingzones tussen natuurgebieden, de negatieve effecten van versnippering tegen te gaan. De inrichting van ecologische verbindingzones is vooral gericht op grotere dieren. Er wordt vanuit gegaan dat planten wel meeprofiteren,

maar veel verbindingszones zijn waarschijnlijk niet voldoende effectief voor planten. Naast statische verbindingselementen als habitat zijn ook 'mobiele verbindingen' nodig voor zaadtransport (de dispersie-infrastructuur voor planten).

Het belang van water als dispersievector kan vergroot worden door maatregelen te nemen die rivieren en beken meer ruimte geven binnen hun stroomgebied. Dit kan leiden tot een meer natuurlijke, gedempte overstromingsdynamiek, in plaats van de huidige overstromingsdynamiek die vaak meer weg heeft van een doortrekkende wc. Vooral plantensoorten drogere delen in het landschap die slechts incidenteel overstromen, zoals zandige oeverwallen, zullen hiervan profiteren.

Het transport van zaden via de vacht van grote zoogdieren kan verbeterd worden door het stimuleren van de uitwisseling van grote zoogdieren tussen (deel)gebieden. Het kan hierbij gaan om wilde dieren, maar ook om gescheperd vee. Een belangrijk middel hierbij is de aanleg van brede en gevarieerde ecologische verbindingszones tussen grote natuurgebieden. Deze 'robuuste verbindingszones' vergroten de ruimtelijke samenhang tussen leefgebieden en bieden voldoende ruimte en habitatvariatie voor migratie van grote zoogdieren. Dergelijke verbindingszones kunnen echter maar een beperkt deel van Nederland (en Europa) bestrijken.

Versterking van de dispersie-infrastructuur in het agrarische gebied kan het ecologisch rendement van natuurgebieden en robuuste verbindingszones vergroten. Nieuwe vormen van agrarisch natuurbeheer, zoals 'boeren voor natuur', kunnen hier aan bijdragen. Dit geldt vooral als de door boeren extensief beheerde gebieden aansluiten op bestaande natuurgebieden, ze ruimtelijk geclusterd voorkomen en ze voldoende continuïteit van beheer hebben. Deze nieuwe vormen van landbouw zijn echter alleen duurzaam als er ook een economische drager is voor deze activiteiten. Indien bij de gangbare, intensieve landbouw de 'ecologische kosten' van het landgebruik op natuur en milieu meegewogen worden in de prijs van producten, dan is 'boeren voor natuur' waarschijnlijk niet alleen ecologisch, maar ook economisch duurzamer. Zowel bij de vermessing als bij de verarming van de dispersie-infrastructuur in ons huidige landschap heeft de landbouw een belangrijke rol gespeeld. De landbouw heeft echter ook de vegetatie in de loop der eeuwen voor een belangrijk deel vormgegeven. Paradoxaal genoeg ligt de sleutel tot het succes van herstelprojecten eveneens voor een deel bij de landbouw.



Dankwoord / Acknowledgements

Wereldwijd staat de biologische diversiteit (biodiversiteit) onder druk. Het keren van deze trend blijkt in de praktijk een lastige opgave. De Nederlandse Organisatie voor Wetenschappelijk Onderzoek (NWO) wil hier via het Stimuleringsprogramma Biodiversiteit een bijdrage aan leveren. De ontwikkeling en vermeerdering van kennis over biodiversiteit kan de efficiëntie van het behoud en herstel van de biologische rijkdommen vergroten. Dit promotieonderzoek vormt een klein onderdeel van dit grotere geheel.

Het project vormde een driehoeksverhouding tussen de Radboud Universiteit Nijmegen (waar ik aangesteld was), Alterra (waar ik gedetacheerd was) en de Rijksuniversiteit Groningen. Hoewel ik in het begin enige neiging tot schizofrenie heb moeten onderdrukken, heb ik deze samenwerking als zeer stimulerend ervaren. Bij de inhoudelijke begeleiding van het onderzoek hebben Jan van Groenendaal, Joop Schaminée, Jan Bakker en Renée Bekker ieder op eigen wijze, maar steeds op een zeer betrokken manier bijgedragen aan dit boekje. Ik kreeg veel ruimte om mijn eigen gang te gaan en ik ben blij met het vertrouwen van jullie in de goede afloop. Jan van Groenendaal, ondanks de grote werkdruk kon ik altijd bij je terecht voor grondig en waardevol commentaar en je was er als dat nodig was. Je enthousiasme over het onderwerp en je scherpe theoretische blik hierop hebben me zeer geïnspireerd. Ook stimuleerde je het contact met diverse ander onderzoekers in binnen en buitenland. Jan Bakker, ook bij jou kon ik altijd terecht voor zeer vlot commentaar op m'n tussenproducten. Verder bewaar ik goede herinnering aan de excursie naar Öland, samen met Eddy van der Maarel, waar ik ook ongegeneerd naar vogels kon kijken. Renée, ik waardeer je grote inhoudelijke en persoonlijke betrokkenheid bij dit project zeer. Je opgewekte levenshouding heeft sterk bijgedragen aan het werkplezier aan dit project. Joop, ik ben trots dat ik je eerste promovendus als kersverse hoogleraar mag zijn. Je hebt me zeer gastvrij binnen je groep ontvangen en me veel ruimte geboden om ook aan andere interessante projecten mee te werken. Ik heb het als een groot voorrecht ervaren om te kunnen werken met de Landelijke Vegetatie Databank.

Mijn dagelijkse collega's op Alterra van het Centrum Ecosystemen zorgden voor een prettige werkplek en dat komt zeker ook door m'n kamergenoot, Rik Huiskes en niet te vergeten door de zorgzame ondersteuning vanuit het secretariaat (Nelja Schonthal, Suze Landman en Liesbeth Steenhuisen). Hoewel ik slechts af en toe in Nijmegen kwam heeft de ondersteuning van José Broekmans sterk bijgedragen aan de gastvrije sfeer. Ed Hazebroek en Nina Smits hielpen bij het veldwerk in de Drentsche Aa, maar zorgden ook daarbuiten voor veel gezelligheid. Ik zal het paardrijden in Brazilië niet snel vergeten. Nina en Rik durfden het gelukkig aan om op te treden als paranimfen. Een speciaal woord van dank voor Stephan Hennekens voor het programmeren van m'n soms obscure wensen in

SynBioSys. Als er ooit een Nobelprijs voor de plantensociologie komt, dan ben jij een goede kandidaat. Ook diverse studenten hebben bijgedragen aan dit project: Bjørn van den Boom, Alex Witten, Stephan te Velde en Thomas Wezendonk.

Ook vele andere collega's hebben via inspirerende discussies bijgedragen aan dit proefschrift en zonder volledig te zijn dank ik hiervoor: Jelte van Andel, Leon van den Berg, Rienk-Jan Bijlsma, Roland Bobbink, Ger Boedeltje, Cajo ter Braak, Bob Bunce, Verena Cordlandwehr, Albert Corporaal, Herbert Diemont, Rudy van Diggelen, Edu Dorland, Werner van Eck, Carla Grashof-Bokdam, Phil Grime, Geert Groot Bruinderink, Ab Grootjans, Rense Haveman, Frank Hoffmann, Rik Huiskes, John Janssen, Felix Knauer, Irma Knevel, Koen Kramer, Hans de Kroon, Loek Kuiters, Ger Londo, Eddy van der Maarel, Dick Melman, Maarten Mouissie, Bob Peet, Dick Pegtel, Andreas Prinzing, Jan Roelofs, John Rodwell, Raymond Schrijver, Henk Siepel, Nina Smits, Merel Soons, Theo Spek, Anton Stortelder, Wil Tamis, Ken Thompson, Philippine Vergeer en Eddy Weeda, de leden van de leescommissie: Phil Grime, Paul Opdam en Jan Roelofs. Het internationale karakter van het ecologisch onderzoek bracht me op diverse symposia in het buitenland, maar met Anton Stortelder als reisgenoot is het werk zelfs in uithoeken als Brazilië en Nieuw Zeeland prima uit te houden.

Dit project zou onmogelijk zijn zonder de veldgegevens die bijeengebracht zijn door vele honderden mensen (o.a. Plantensociologische Kring Nederland, Stichting FLORON, Provincie Drenthe). Dit proefschrift kan dan ook gezien worden als een eerbetoon aan al deze mensen. De eerste twee jaar leek het samenstellen van de database met planteneigenschappen een eindeloos project. Van veel soorten bleken gegevens over basale eigenschappen nauwelijks voorhanden of verstopt in onbekende tijdschriften en stammend uit de periode dat tijd nog niet gelijk stond aan geld. Gelukkig bleken diverse collega's bereid gegevens uit te wisselen. Voor het vullen van de grootste overgebleven gaten werden zaden verzameld van ruim 250 zeldzame soorten. Ook hierbij heb ik hulp gekregen van vele mensen, die daarmee een belangrijke bijdrage hebben geleverd aan de dispersie database (hoofdstuk 2): Piet Bremer, John Bruinsma, Eeuwe Dijk, Bas van Gennip, Rense Haveman, Bas Kers, Ger Londo, René van Moorsel, Joop Schaminée, Nina Smits, Merel Soons, Harold Steendam, Yzaak de Vries en Ruud van der Meijden die het verschijnen van dit proefschrift helaas niet heeft mogen meemaken.

Statistische adviezen werden gegeven door: Cajo ter Braak, Matthias Löwe, Patsy Haccou, Georgos Martakis en Bert van der Werf. Het engelse van diverse hoofdstukken is gestroomlijnd door Jan Klerkx, terwijl Dick Visser de lay-out en vormgeving heeft verzorgd. Fraaie foto's werden geleverd door Ed Hazebroek, Luc Hoogenstein, Ruud Knol, Gernot Pohl en Diana Terwisscha.

I would like to thank all people involved in the EU project LEDA and the ESF project ASSEMBLE for the exchange of information and the stimulating discussions. Besides the people involved in these projects, there were many other people who provided data, especially: Otto Brinkkemper (National Service for Archaeo-

logical Heritage), Eric Cosyns (University of Gent), Wilma Gijsbers (Meertens Instituut, provided figure 1 in Box 3), Ingolf Kühn (Helmholtz Centre for Environmental Research – UFZ, Germany), Maud von Lampe (University of Applied Science, Anhalt, Germany), Robin Pakeman (Macaulay Institute Aberdeen). Prof. Dr. H. Sukopp (Technical University Berlin), Wil Tamis (University of Leiden). Furthermore I had stimulating co-operations with colleagues abroad, including Andreas Prinzing (University of Rennes, France), James Van Kley (Stephen F. Austin State University, USA), Walter Durka (Helmholtz Centre for Environmental Research – UFZ, Germany) and Sabine Tischew and Anita Kirmer (University of Applied Science, Anhalt, Germany). Andreas introduced me in the intriguing world of phylogenetics and Sabine and Anita kindly showed us the mining areas near Halle (the largest seed traps I have ever seen).

Mijn ouders, Bé en Dineke, hebben me de vrijheid gegeven om m'n eigen weg te gaan en me daarbij altijd gesteund. In m'n vroege jeugd heeft Bé me al enthousiast gemaakt voor de natuur en me wegwijs gemaakt in de vogelzang. De verwondering voor de natuur is nog verder aangewakkerd bij de NJN en ik bewaar dierbare herinneringen aan de vele gezamenlijke fietsvakanties. De natuur is gelukkig meer dan alleen koele grafieken en tabellen! Het wordt weer hoog tijd voor een ouderwetse Schier reünie.

Het leven van een promovendus bestaat gelukkig niet alleen uit lange werkdagen. Mijn vrienden, familie en burens van de Boerlaan zorgden voor een welkome afwisseling. In een onbewaakt ogenblik heb ik op m'n cv gezet dat ik hobbyboer ben, met als onvoorziene consequentie dat er geen excuus meer was om niet 's nachts het bed uit te moeten in de lammerentijd. De veestapel zorgde op m'n thuiswerkdagen in elk geval wel voor een effectief anti-RSI beleid. Schapen drijven met het enfant terrible, Lynn, mag wat mij betreft genomineerd worden voor de olympische spelen. Lieve Diana, zonder je warme liefde was het werk aan dit boekje een stuk zwaarder geweest. De afgelopen jaren beloven veel moois voor de toekomst!

Wim

Harenermolen, herfst 2007



Curriculum vitae

Op 16 augustus 1971 ben ik geboren in Utrecht. Veel van mijn veldkennis heb ik opgedaan bij de Nederlandse Jeugdbond voor Natuurstudie. Hoewel mijn interesseveld breed is (vogels, insecten, paddenstoelen en planten), heb ik uiteindelijk gekozen voor een specialisatie als plantenecoloog. In 1996 heb ik mijn studie biologie aan de Rijksuniversiteit Groningen afgerond. Tijdens mijn doctoraalonderzoeken heb ik gekeken naar de bestuiving van Duifkruid in relatie tot populatiegrootte, de groei van blauwgraslandplanten o.i.v. fosfaatfixatie door ijzer en ijzer-toxiciteit en de soortenrijkdom van planten o.i.v. bodemheterogeniteit en mycorrhizaschimmels.

Van 1996 tot 2000 heb ik gewerkt bij het ecologisch adviesbureau Buro Bakker. Hierbij heb ik veel veldwerk verricht en veel ecosystemen beter leren kennen. In maart 2000 ben ik bij de Radboud Universiteit Nijmegen begonnen aan het project dat geleid heeft tot dit proefschrift. Ik was hierbij gedetacheerd bij Alterra in Wageningen. Dit promotieproject vormde een onderdeel van het NWO Stimuleringsprogramma Biodiversiteit. Na afloop van dit project heb ik van 2005 tot 2006 als junior onderzoeker (post-doc) gewerkt aan een project van de Europese Commissie (LEDA). Vanaf 2006 ben ik voor 50% aangesteld bij de Radboud Universiteit Nijmegen als post-doc voor een project van de European Science Foundation (ASSEMBLE) en voor de andere 50% bij Alterra, Centrum Ecosystemen.

In 2006 heb ik voor een jaar plaats genomen in de editorial board van het nieuwe, internationale tijdschrift 'Ecological Informatics' en was lid van het 'program committee of the 5th International Conference on Ecological Informatics' in december 2006 in Santa Barbara, USA met het thema 'Novel computational techniques for improved management, understanding and forecasting of complex ecological data'. Verder ben ik thuis, samen met Diana Terwisscha, actief als hobbyboer.

Publications

Publications in international peer reviewed journals

- Ozinga, W.A., S.M. Hennekens, J.H.J. Schaminée, N.A.C. Smits, R.M. Bekker, C. Römermann, L. Klimeš, J.P. Bakker & J.M. Van Groenendaal (2007). Local aboveground persistence of vascular plants: Life-history trade-offs and environmental constraints. *Journal of Vegetation Science* 18: 489-497.
- Schaminée, J.H.J., S.M. Hennekens & W.A. Ozinga (2007). Use of the ecological information system SynBioSys for the analysis of large datasets. *Journal of Vegetation Science* 18: 463-470.
- Boedeltje, G., W.A. Ozinga & A. Prinzing (2007). The trade-off between vegetative and generative reproduction across Angiosperms influences regional hydrochorous propagule pressure. *Global Ecology and Biogeography* (in press)
- Van Bodegom, P.M., Grootjans, A.P., Sorrell, B.K., Bekker, R.M., Bakker, C. & Ozinga, W.A. (2006). Plant traits in response to raising groundwater levels in wetland restoration: evidence from three case studies. *Applied Vegetation Science* 9: 251-260.

- Ozinga, W.A. S.M. Hennekens, J.H.J. Schaminée, R.M. Bekker, A. Prinzing, S. Bonn, O. Tackenberg, P. Poschlod, K. Thompson, J.P. Bakker & J.M. van Groenendaal (2005). Assessing the relative importance of dispersal in plant communities using an ecoinformatics approach. *Folia Geobotanica* 40: 53-68.
- Ozinga, W.A., J.H.J. Schaminée, R.M. Bekker, S. Bonn, P. Poschlod, O. Tackenberg, J.P. Bakker & J.M. van Groenendaal (2005). Predictability of plant species composition from environmental conditions is constrained by dispersal limitation. *Oikos* 108: 555-561.
- Soons, M.B. & W. A. Ozinga (2005). How important is long-distance seed dispersal for the regional survival of plant species? *Diversity and Distributions* 11: 165-172.
- Ozinga, W.A., R.M. Bekker, J.H. J. Schaminée & J.M. Van Groenendaal (2004). Dispersal potential in plant communities depends on environmental conditions. *Journal of Ecology* 92: 767-777.
- Prinzing, A. W.A. Ozinga & W. Durka (2004). The relationship between global and regional distribution diminishes among phylogenetically basal species. *Evolution* 58: 2622 – 2633.
- Schaminée, J.H.J., J.E. van Kley & W.A. Ozinga (2002). The analysis of long-term changes in plant communities: case studies from the Netherlands. *Phytocoenologia* 32: 317-335.
- Ozinga, W.A., J. van Andel & M.P. McDonnell-Alexander (1997). Nutritional soil heterogeneity and mycorrhizas as determinants of plant species diversity. *Acta Botanica Neerlandica* 46: 237-254.
- Baar, J., W.A. Ozinga & Th.W. Kuyper (1994). Spatial distribution of *Laccaria bicolor* genets reflected by sporocarps after removal of litter and humus layers in a *Pinus sylvestris* forest. *Mycological Research* 98: 726-728.
- Baar, J., W.A. Ozinga, I.L. Sweers & Th.W. Kuyper (1994). Stimulatory and inhibitory effects of needle litter and grass extracts on the growth of some ectomycorrhizal fungi. *Soil Biology and Biochemistry* 26: 1073-1079.

Manuscripts submitted to international peer-reviewed journals

- Kirmer, A., S. Tischew, W.A. Ozinga, M. von Lampe & J.M. van Groenendaal. Importance of regional species pools and functional traits in colonisation processes. *Journal of Applied Ecology* (in revision)
- Prinzing, A., R. Reiffers, S.M. Hennekens, O. Tackenberg, W.A. Ozinga, J.H.J. Schaminée, W.G. Braakhekke & J.M. van Groenendaal. Less lineages – more trait variation: phylogenetically clustered Angiosperm communities are functionally more diverse. *Ecology Letters* (in revision).
- Ozinga, W.A., C. Römermann, R.M. Bekker, A. Prinzing, W.L.M. Tamis, J.H.J. Schaminée, S.M. Hennekens, K. Thompson, P. Poschlod, M. Kleyer, J.P. Bakker & J.M. van Groenendaal. Dispersal failure contributes to plant losses in NW Europe. (submitted).
- Colles, A., S.M. Hennekens, W.A. Ozinga, J.H.J. Schaminée & A. Prinzing. Will the decline of specialists affect future diversification? (submitted).
- Kleyer, M., R.M. Bekker, I.C. Knevel, J.P. Bakker, K. Thompson, M. Sonnenschein, P. Poschlod, J.M. van Groenendaal, L. Klimeš, J. Klimešová, S. Klotz, G.M. Rusch, M. Hermy, D. Adriaens, G. Boedeltje, B. Bossuyt, A. Dannemann, P. Endels, L. Götzberger, J.G. Hodgson, A-K. Jackel, I. Kühn, D. Kunzmann, W.A. Ozinga, C. Römermann, M. Stadler, J. Schlegelmilch, H.J. Steendam, O. Tackenberg, B. Wilmann, J.H.C. Cornelissen, O. Eriksson, E. Garnier, B. Peco. The LEDA Traitbase: A database of life-history traits of Northwest European flora. *Journal of Ecology* (Submitted)
- Louette, G., D. Maes, J.R.M. Alkemade, L. Boitani, J. Eggers, A. Falcucci, E. Framstad, W. Hagemeijer, S.M. Hennekens, L. Maiorano, S. Nagy, A. Nieto Serradilla, W.A. Ozinga, J.H.J. Schaminée, V. Tsiaousi, S. van Tol & B. Delbaere. Cost-effective assessment of policy impact on biodiversity using species sensitivity scores. (submitted)

Other publications

- Ozinga, W.A., M. Bakkenes & J.H.J. Schaminée (2007). Sensitivity of Dutch vascular plants to climate change and habitat fragmentation; A preliminary assessment based on plant traits in relation to past trends and future projections. *Wettelijke Onderzoekstaken Natuur & Milieu, WOt-report 49*, Netherlands Environmental Assessment Agency.
- Janssen, J.A.M., A.H.P. Stumpel, R.J. Bijlsma, I. Keizer-Sedlakova, A.T. Kuiters, F.G.W.A. Otterburg, W.A. Ozinga, J.H.J. Schaminée & H.N. Siebel (2007). Internationaal belang van de nationale natuur; Ecosystemen, Vaatplanten, Blad- en Levermossen, Zoogdieren, Reptielen, Amfibieën en Vissen. Wageningen, Wettelijke Onderzoekstaken Natuur & Milieu, *WOt-rapport 43*.
- Schrijver, R.A.M., W.A. Ozinga & W.H. Diemont (2007). Payments for pastoral landscapes of Europe. In: A.P. Grootjans & L. Wolejko (editors). Multifunctional use of Polish peatlands.
- Schrijver, R.A.M., D.P. Rudrum, W.H. Diemont, W.A. Ozinga & T.J. de Koeijer. (2007). Cost price calculations as the basis of conservation payments for marginal land in the case of No External Input farm systems. (in press).
- Baar, J. & W.A. Ozinga (2007). Mycorrhizaschimmels, sleutelfactor voor duurzame landbouw en natuur. KNNV Uitgeverij, Zeist.

- Weeda, E.J., W.A. Ozinga & G.A.J.M. Jagers op Akkerhuis (2006). Diversiteit hoog houden; Bouwstenen voor een geïntegreerd natuurbeheer. *Alterra-rapport* 1418.
- Ozinga, W.A. & J.H.J. Schaminée, eds. (2005) Target species – Species of European concern. A data-base driven selection of plant and animal species for the implementation of the Pan European Ecological Network. Wageningen, Alterra, *Alterra-report* 1119.
- Ozinga, W.A. & J.H.J. Schaminée (2004) The development of ecological information systems, a new tool in biological research. In: *Recent Res. Devel. Environ. Biol.* pg. 531-551.
- Tamis, W.L.M., R. van der Meijden, J. Runhaar, R.M. Bekker, W.A. Ozinga, B. Odé & I. Hoste (2004). Standaardlijst van de Nederlandse flora 2003. *Gorteria* 30(4/5): 101-195.
- Bakker, J.P., R.M. Bekker, W.A. Ozinga & M. Wallis de Vries (2003). Er zit te weinig beweging in de Ecologische Hoofdstructuur. *De Levende Natuur* 104: 261-266.
- Bekker, R.M., J.P. Bakker, W.A. Ozinga & K. Thompson (2003). Seed traits: essential for understanding seed longevity. *Aspects of Applied Biology* 69: 1-9.
- Janssen, J.A.M., W.A. Ozinga & J.H.J. Schaminée (2003). Europese natuur in Nederland. Monitoring van habitattypen – een verkenning. *Alterra-rapport* 841.
- Ozinga, W.A. & E. Arnolds (2003). Mycorrhizapaddestoelen als leidraad voor beheeradviezen voor bossen op voedselarme zandgrond. *De Levende Natuur* 104: 177-183.
- Bakker, J.P. Bekker, R.M., J.M. Van Groenendaal, Ozinga, W.A., J.H.J. Schaminée, S.M. Hennekens, R. Van der Meijden & W. Tamis. (2002). Predicting plant biodiversity in changing Dutch landscapes. *Newsletter Stimulation Programme Biodiversity* 5: 8-12.
- Ozinga, W.A. & D.B. Terwisscha (2001). Paddestoelen als doelsoorten voor zeldzame bostypen. *Vakblad Natuurbeheer* 40: 99-101.
- Ozinga, W.A. (2001). Paddestoelenkartering Dwingelderveld 1999/2000. Buro Bakker in opdracht van Provincie Drenthe.
- Bakker, N.J., H.A. Inberg, W.A. Ozinga, J.E. Plantinga & M. van Tweel (2001). Vegetatiekartering Terschelling 1998-1999. Buro Bakker in opdracht van SBB Friesland.
- Ozinga, W.A., H.A. Inberg & N.J. Bakker (2000). Vegetatiekartering Vijlener Bossen en Platte Bossen 1997. Buro Bakker in opdracht van SBB Hollands Noorden.
- Ozinga, W.A. (1999). Vegetatiekartering van bossen in ZW-Friesland. Buro Bakker in opdracht van SBB Friesland.
- Ozinga, W.A. (1999). Vegetatiekartering Engbertsdijkvenen 1997. Buro Bakker in opdracht van SBB Overijssel.
- Ozinga, W.A. (1999). Beheervisie vestiging Loenderveen. Buro Bakker in opdracht van Waterleidingmaatschappij Amsterdam.
- Ozinga, W.A. (1999). Beheersplan Terra Nova e.o. Buro Bakker in opdracht van Provincie Utrecht.
- Ozinga, W.A. (1998). Vegetatiekartering Dwingelderveld. Veranderingen tussen 1983 en 1997. Buro Bakker adviesburo voor ecologie, in opdracht van Provincie Drenthe.
- Bakker, L. & W. Ozinga (1997). Zand, klei of allebei? Soortendiversiteit van paddestoelen op landgoed Vennebroek. *Amoeba* 71: 180-183.
- Bakker, N.J. & W.A. Ozinga (1997). Vegetatiekartering De Dennen 1996. Buro Bakker adviesburo voor ecologie, in opdracht van SBB Hollands Noorden.
- Bakker, N.J. & W.A. Ozinga (1997). Vegetatiekarteringen in de regio Veluwe-Achterhoek: Terlet en Roozendaal. Buro Bakker adviesburo voor ecologie, in opdracht van SBB Veluwe-Achterhoek.
- Ozinga, W.A. & J. Baar (1997). Primaire Grove-dennenbossen in stuifzandgebieden als refugium voor zeldzame mycorrhizapaddestoelen. *De Levende Natuur* 98: 129-133.
- Ozinga, W.A. (1997). Vegetatiekartering Jutjesriet 1996. Buro Bakker adviesburo voor ecologie, in opdracht van SBB Overijssel.
- Ozinga, W. (1995). *Coprinus sclerotiger*, nieuw voor Nederland. *Coolia* 38: 17-19.
- Ozinga, W. & L. Bakker (1994). Pilze in de Eifel; kalk als oorzaak voor grote rijkdom aan mycorrhizapaddestoelen. *Kruipnieuws* 57: 18-23.
- Ozinga, W., L. Bakker & M. Klasberg (1994). Bijzondere paddestoelenflora in stuifzandgebieden bij Havelte. *Amoeba* 68: 70-71.
- Tieleman, I. & W. Ozinga (1994). Vegetatieontwikkeling in stuifduinen op Schiermonnikoog. *Amoeba* 68: 98-99.
- Baar, J., W.A. Ozinga & Th.W. Kuyper. (1993). Ectomycorrhizal succession in Scots pine forests: the role of *Deschampsia flexuosa*. In: *European Forests Reserves* (Eds. M.E.A. Broekmeyer, W. Vos & H. Koop), pp. 249-254. Pudoc, Wageningen.
- Ozinga, W. (1993). Vegetatieveranderingen in Drentse vennen na hydrologische beheersmaatregelen. Provincie Drenthe, afdeling Ruimte en Groen.
- Ozinga, W. (1993). Kolonisatie van geplagde proefvlakken in Grove Dennenbossen door *Laccaria bicolor*. Biologisch Station Wijster, LUW.
- Ozinga, W. (1993). Invloed van strooisel van *Deschampsia flexuosa* op de groei van ectomycorrhizaschimmels. Biologisch Station Wijster, LUW.
- Ozinga, W. (1991). Biotoopvoorkur bij zweefvliegen; een vergelijking van enkele biotopen in de Hortus van Haren. *Amoeba* 65: 152-153.

