Operationalising resilience for ecosystem management

by assessing ecosystems' adaptive capacity

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Operationalising resilience for ecosystem management by assessing ecosystems' adaptive capacity

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Contents

Chapter one

Introduction: operationalizing resilience for ecosystem management in a rapidly changing world

1.1 Transition in ecosystem management

Ecosystems are under increasing pressure driven by both climate change and socio-economic developments such as land-use change. The impacts on biodiversity are increasingly recognized and, with this, the need to adjust the goals of ecosystem management and policy. Currently, a frequent, perhaps universal tendency in ecosystem management is to reduce the range of natural system variation in an attempt to increase the predictability and reliability of ecosystem services provision (Holling and Meffe 1996). For example, people remove predators to increase the number of game and suppress forest fires to sustain a steady wood supply. In response to environmental change, unpredicted natural disasters, such as devastating fires and erosion events, can follow (see examples in Renkin and Despain 1992; Gunderson 2000; Turner et al. 2003). An increasing consensus emerges recognizing that all the dynamic pressures to which ecosystems are subjected, call for a transition in ecosystem management and conservation, away from approaches that have static conservation objectives assigned to sites, as is the case for example with the European Union's Natura 2000 network(Wu and Loucks 1995; Turner 2010; Mori 2011; Prober and Dunlop 2011; Standish et al. 2014; van Teeffelen et al. 2014). Instead, ecosystem management and conservation requires approaches that build on dynamic views of ecosystems and changing environmental conditions as a central guiding principle towards more adaptive management and conservation strategies. These new approaches help to cope with the increasing human pressures like land-use change.

The response of ecosystems to change is contained in the 'ecological resilience' concept. Resilience is discussed extensively in recent literature, but it has to be made operational for application in ecosystem management. Resilience is defined as the capacity of an ecosystem to absorb disturbances, reorganize and maintain its adaptive capacity (Carpenter et al. 2001, Gunderson 2000). This adaptive capacity is often related to the role of biodiversity in maintaining ecosystem functioning (Walker 1992, 1997, Tilman 1996; Norberg et al. 2001; Elmqvist et al. 2003). Ecosystem functioning reflects species activities and the effects these activities have on the biological and chemical conditions characteristic for an ecosystem. A forest ecosystem, for example, exhibits rates of plant production, carbon storage, and nutrient cycling that are characteristic of most forests. If the forest is converted to an agroecosystem, its functioning changes. The biodiversity *insurance hypothesis* (c.f. Yachi and Loreau 1999) states that biodiversity insures ecosystem functioning because many species better guarantee that some will maintain functioning if others fail. Additionally, the *redundancy hypothesis* (Walker 1991; Lawton and Brown 1993; Vitousek and Hopper 1993) assumes that up to a point, species redundancy (the number of species playing a similar ecological role) enhances ecosystem resilience, especially under changing environmental conditions. Accumulating evidence suggests that the effects of species diversity on ecosystem functioning depend on the spatial scale (Peterson et al. 1998; Loreau et al. 2001). That ecosystem resilience therefore should be linked to spatial characteristics of the landscape is increasingly acknowledged (Holling 1973; Wiens 1989; Virah-Sawmy et al. 2009, Oliver et al. 2010). The question, however, is how this perspective on resilience can take us beyond simply conserving species diversity to an effective adaptive ecosystem management based on ecosystem resilience in a changing world.

1.2 An exploration of the resilience concept

Resilience is thus a popular concept to understand the adaptive capacity of ecosystems to uncertainty and surprises, both in scientific research and in policy development. The number of publications with ‘ resilience’ in the title increases and related terms like ‘robustness’ and ‘sustainable’ can be found in environmental policy strategies, such as the 7th Environment Action Programme and the European Union’s Biodiversity Strategy (EC, 2011b; EEA, 2012). Even so, resilience is often poorly defined and/or used inconsistently. When lacking a consistent conceptual framing, applying resilience can result in fuzzy management applications. To make resilience operational for ecosystem management and policy we therefore need to define, conceptualize and operationalize resilience in specific contexts. As Carpenter et al. (2001) rightly emphasized, applying resilience to concrete situations requires that we answer their question “Resilience of what to what?”. We need to identify the state and spatial scale of an ecosystem (i.e. Resilience *of what?*), and the disturbances that affect the ecosystem through time (i.e. Resilience *to what?*). Disturbances in this context, as defined by Chapin et al. (2002), are "a relatively discrete event in time and space that alters the structure of populations, communities and ecosystems and causes changes in resources availability or the physical environment".

In ecology, the origin of resilience dates back to the 1960-ies and 1970-ies . The seminal paper of Holling (1973) was the first that emphasized the consequences of two different definitions of resilience for ecosystems (Figure 1.1). The first definition uses system resistance to disturbance and speed of return to the equilibrium to measure resilience (Pimm 1984; O'Neill et al. 1986; Tilman and Downing 1994). This definition is named ’engineering’ resilience and focuses on efficiency, constancy and predictability. These three elements are the core of a command-and-control management philosophy. This approach considers spatial and temporal system dynamics as perturbations to an otherwise stable system. The second definition emphasizes the magnitude of disturbances that can be absorbed before a system flips to another stable equilibrium (Holling 1973, 1994). This is known as ‘ecological’ resilience and focuses on persistence, change and unpredictability - elements embraced by an adaptive management philosophy. The latter definition considers system dynamics in time and space as inherent properties of ecosystems.

Whether a stable equilibrium is wanted or not, depends on the ecosystem’s desired social or economic values and on the management perspective. Therefore, different indicators are used to measure resilience (Carpenter et al. 2001; Allen et al. 2011). A great variety of (un)wanted stable equilibriums have been documented for lakes, coral reefs, marine fisheries, benthic systems, wetlands, forests, savannahs and rangelands (Carpenter et al. 2001; Scheffer et al.

2001). All these examples emphasize that ecosystems comprise interactions between slow and fast processes, and between local, regional and global processes. Those interactions are often non-linear and maintain biodiversity through biotic and abiotic variability. All this influences the resilience of ecosystems. Consequently, resilience at a certain time or at a particular location can affect the resilience later or elsewhere. The size of stability domains typically depends on slowly changing variables, such as land use, nutrient stocks, soil properties and biomass of long-lived organisms. Insights gained from the case studies (ibid) imply that, to prevent unwanted state shifts, management best focusses on the gradual environmental changes that affect resilience, rather than control unpredictable disturbances.

Figure 1.1. Schematic representation of (a) engineering resilience, and (b) ecological resilience. The black balls show acceptable conditions and grey balls show unacceptable conditions. Dashed arrows represent resistance to disturbance and speed of return to the equilibrium as measures of resilience. Solid arrows represent the trajectory of a system into other stability domains.

1.3 Resilience is more than the sum of its parts

Although engineering and ecological resilience are fundamentally different, both definitions assume that the system returns to a stable equilibrium. The emphasis on returning to a specific equilibrium dominates the literature (e.g., Cousins et al. 2003; Enright et al. 2014) and the resulting insights shape the often short-term management measures applied to a particular aspect of an ecosystem to a particular type of disturbance (Folke et al. 2010; Desjardins et al. 2015). Present ‘resilience thinking’ (Walker and Salt, 2006) challenges the whole idea of stable equilibria and advocates that systems may change over time with or without an external disturbance (Scheffer 2009). This emerging perspective conceives resilience as the ability to transform: to allow the (eco)system to operate under different driving processes (Carpenter et al. 2005). This interpretation fits the current knowledge of ecosystems dynamics across multiple spatial and temporal scales best (e.g., hierarchical patch dynamics, with no proportional or linear relationship between the causes and the effects; Diez and Pulliam, 2007). Such a view of resilience reflects a shift in how scientists think about ecosystem dynamics. Rather than seeing ecosystems as orderly and predictable, they experience them as complex and demonstrating surprising behaviour. In itself this is not a evolutionary idea but what is new is the acknowledgment that “past behaviour of the system is no longer a reliable predictor of future behaviour even when circumstances are similar” (Duit et al. 2010).

This perspective thus challenges the adequacy of conventional ecosystem management reducing natural variability to increase the predictability of natural resources for human use. A shift to managing for resilience advocates that resilience is no longer viewed as a descriptive property of a system, but as a normative property: a capacity that should be achieved and promoted. In the scientific literature a number of ecosystem properties that support management to operationalize resilience, are discussed. All proposed management actions, such as promoting connectivity and spatial heterogeneity (e.g., Opdam and Wascher 2004; Mori et al. 2013) highlight the possibilities of species to reorganise. In this thesis, I focus on adaptive capacity, i.e. the capacity of ecosystems to reorganize after disturbances. From the ecosystem functioning perspective, there is a growing consensus that the loss of a species per se does not necessarily have obvious functional consequences. Rather, the species composition and its specific ecological role captured by species traits is associated with resilience (Peterson et al. 1998; Van Ruijven and Berendse 2010; Laliberté et al. 2010; Mouillot et al. 2013). Following recent insights about the relationship between adaptive capacity and the diversity of such species traits, I will analyse how the composition of species traits present in an ecosystem determines species’ responses to changing environmental conditions and their effect on the reorganization of that ecosystem (Section 1.7).

I investigate these responses by using available plant data. Plant trait databases are well developed and plant traits are extensively described in different contexts (e.g., Cornelissen et al., 2003; Lavorel and Garnier 2003; Diaz et al. 2004; Ruijven and Berendse, 2010; Section 1.4). To know how ecological processes at different spatial scales generate adaptive capacity, I consider the impact of environmental variables on species traits at localities or sites and in wider landscapes (Sections 1.4 and 1.5). Due to the multi-dimensional nature of the resilience concept, how different ecosystems can maintain resilience is not obvious. I use the adaptation strategies of plant species and the interactions between species, disturbance regimes and landscape structures to gain insight into the elements that reflect changes in adaptive capacity (Section 1.6). Such an insight can be used by managers and decision makers to identify strategies for the long term.

1.4 Using plant traits as a proxy of adaptive capacity

Predicting how communities might respond to disturbances that change over landscape gradients or vary among different habitats, is for many reasons fraught with uncertainty. Disturbance regimes are known for their multiple dimensions, such as their frequency, intensity, duration and spatial extent (e.g., Van Teeffelen et al. 2012), and plant species respond differently to disturbance events because of differences in plant life-history traits, such as survival, fecundity and colonisation capacity (Schippers et al. 2001). One useful attempt to capture this variability is a trait-based approach incorporating widely-available information about species’ biology and look for consistent responses within species groups that share traits. This can help to reduce uncertainty about how species respond to disturbance (Henle et al. 2004). Functional traits capture fundamental trade-offs and determine species’ ecological roles. The trade-off between the number of seeds produced and the size of each individual seed, for example, supplies information about reorganization processes in an ecosystem. Large seeds provide robust seedlings able to succeed where competition is high and resources are scarce, but these seeds can only be produced in relatively small numbers. In contrast, small seeds fail where competition is high, but can be produced in high numbers increasing the chance of dispersal to suitable sites with few competitors and appropriate resource availability. Thus, seed size is an easily measured plant trait that likely provides insight into the relative contribution of dispersal and competitive processes to resilience. The fundamental assumption is that because of trade-offs, traits that lead to success in one environment do not lead to similar successes in other environments (Craine 2009). Thus, understanding how traits vary with the environment and with each other helps to predict general patterns and provides a mechanistic link between disturbances and response patterns within communities. As such, the resulting knowledge on communities’ responses to disturbances can be of great value when ecosystem managers face decisions associated with sites and landscapes or environmental changes, and how all these influences might impact resilience.

1.5 Landscape structure

Accumulating evidence shows that landscape structure also influences ecological resilience (e.g., Verboom et al. 2010; Mori 2011; Schippers et al. 2015). For example, in relation to species viability Pickett and Thompson (1978) define a “minimum dynamic area” as “... the smallest area with a natural disturbance regime, which maintains internal recolonization sources, and hence minimizes extinction...”. The persistence and dynamics of metapopulations are also determined by the spatial cohesion of the habitat networks in landscapes (Opdam et al. 2006; Verboom et al. 2010; Fronhofer et al. 2012; Campbell et al. 2015). A frequently overlooked property of these habitat networks that can contribute to resilience, is landscape heterogeneity. Such heterogeneity is created by spatial discontinuities in environmental conditions and, from the perspective of a plant species, this creates variability in the distribution of suitable habitat. Moreover, habitat patches vary in suitability; some are more suitable (i.e. higher quality) and provide greater fitness (i.e. the ability to survive and reproduce) to plant species than others. In addition, because landscapes are dynamic, the distribution of suitable habitat varies over time and space, and consequently the distances between them (Peterson 2002). Thus, there is spatio-temporal variation in the availability of suitable habitats in landscapes, which affects the persistence of species in such landscapes (Van Teeffelen et al. 2012). The responses of species to heterogeneity depend on the dynamic interaction between species strategies and environmental conditions. Several studies show that a change in landscape heterogeneity can influence species trait composition by, for instance, changing habitat area, diversity and fragmentation (e.g., Berg et al. 2011; Borschig et al. 2013). With further environmental change projected over the coming century, understanding how resilience is influenced by a consistent relationship between landscape properties and species traits, should be determined. Knowing the potential limits of species reorganization in a landscape is likely to be particularly useful for guiding management efforts.

1.6 Ecological memory

In unmanaged ecosystems, natural selection led to high ecological resilience to natural disturbances. Holling (1973) illustrated the existence of multiple stable equilibriums in natural systems and how they relate to ecological processes, random events and variability at different temporal and spatial scales. Therefore, allowing natural disturbances has been proposed as an effective strategy in ecosystem management (e.g., DeLong and Tanner 1996). The frequency, size and intensity of disturbances then determine the impact on ecosystem states (Turner 2010). The different expressions of species traits under different disturbance regimes produce much of the spatial and temporal variability in species communities. Disturbances are thus key drivers of landscape heterogeneity.

Bengtsson et al. (2003) highlighted the role of spatial and temporal variability in the response of populations to disturbances by introducing the concept of ‘ecological memory’. They define ecological memory as “the network of species, their dynamic interactions between each other and the environment, and the combination of structures that make reorganization after disturbance possible.” Ecological memory is distinguished into an internal and an external component. Internal memory consists of ‘biological legacies’, represented by species presence and their within-patch dynamics defined by, for example, their presence, reproduction and interactions (e.g., competition abilities, trophic relations; Bengtsson et al. 2003) and genetic composition (Schaefer 2009). The external memory is related to between-patch dynamics with external patches functioning as colonization sources after local extinctions (Bengtsson et al. 2003). Ecological memory thus explicitly involves ecological processes at different scales.

Although several studies have examined how ecological memory is encoded in site history and biological legacies, like seedbanks, bud banks and stem fragments (e.g., Sun et al. 2013), and mobile link species that increase ecosystem resilience by connecting habitats and ecosystems as they move between them (Gilbert 1980; Lundberg and Moberg 2003;), the biological implications of ecological memory in terms of mechanisms are poorly understood. With the growing number of trait-based descriptions of plant strategies and the notion that species with homologous traits are expected to respond similarly to environmental filters (Keddy 1992; Suding et al. 2005; Schweiger et al. 2005; Chillo, Anand and Ojeda 2011; Pease et al. 2015), we should be able to understand how communities respond to disturbances in space and time (Figure 1.2). With such knowledge, the relative importance of spatial versus temporal processes for shaping species distributions and community assemblies can be identified (Leibold et al. 2004, Diez and Pulliam 2007; Alexander et al. 2012). Insight into the mechanisms that influence ecological memory, is fundamental to identify planning and management strategies that increase resilience (Schaefer 2009). Especially in human-dominated landscapes where ecological networks gain importance (DeAngelis and Waterhouse 1987; Standish et al. 2014).

1.7 Objectives

As follows from the introduction above, what resilience and ecological memory signify for ecosystem management is not yet clear, beyond the assumption that having resilient ecosystems is good. I think that resilience is an evolving, promising concept to learn how to cope with complexities, uncertainties and surprises, resulting from unpredictable environmental change and ecological responses. But if resilience indeed is a promising concept, what are the opportunities and limitations of interpreting resilience into practice?

The aim of this thesis is therefore to (i) investigate what the interaction between species traits, environmental variability and landscape structure are, (ii) how these interactions contribute to the ecological memory of an ecosystem and (iii) to identify key mechanisms of resilience operating at the level of individual species, populations and communities. The aim is addressed through the following research questions:

1. How to link species traits to local environmental variability to assess resilience?
2. Which interactions between spatial heterogeneity and traits affect resilience?
3. Can species traits be used to identify mechanisms related to an ecosystem’s ecological memory?
4. How does the interaction between environmental variability and landscape structure affect the adaptability and transformability of ecosystems?

1.8 Outline of the thesis

This thesis consists of six chapters (Figure 1.2). In Chapter 2, Suding’s effect-and-response framework was adapted to understand how communities interact with the environment in a wetland ecosystem (Suding et al. 2008). In this framework, local abiotic parameters influence trait composition of the vegetation. The relationship between traits and environmental gradients determined the change in resilience. Conditions for a meaningful selection of effect and response traits are discussed (research question 1). Interpreting the resilience concept as an evolving and multidimensional concept helps to identify different ecosystem properties favouring ecological resilience. This perspective supports the idea that ecological processes contributing to ecological resilience take place across spatial and temporal scales. Chapter 3 tested the role of landscape heterogeneity in trait selection across multiple spatial extents for butterflies and plants in wetlands across the Netherlands. Butterflies and plants follow very different strategies to cope with disturbances and are expected to use the landscape different. A multivariate analyses was used to identify how landscape heterogeneity was related to the different species traits. The approach highlighted the importance of the considered landscape extent for the adaptive capacity of the ecosystem (research question 2). The combination of spatial and temporal variation in an ecosystem selects for species adaptation strategies including trade-offs between survival and establishment. I expect that strategies prefer different environments. Chapter 4 implements a model to study how disturbance regimes at local and landscape-scale shape the internal and external memory of plant communities in a river floodplain system. Combining ecological processes at local and landscape level show that plant traits can identify ecological processes contributing to the ecological memory of a floodplain ecosystem. The outcomes are used to discuss in what way these mechanisms can support ecosystem management (research question 3). In Chapter 5, a demographic spatially-explicit individual-based model is used to explore how interaction between landscape heterogeneity and disturbance regime affect the ecological memory of a floodplain ecosystem. Four adaptation strategies of riparian plants are used to show how the relative strategy abundances change with changing flooding regime along a heterogeneity gradient. The results show the importance of frequent flooding to maintain all strategies. And how large patches positively affect the abundances of strategies with lower dispersal abilities. Chapter 6 integrates the results and synthesize how the mutual relations of environmental variables and landscape structure with species traits provides a mechanistic understanding of resilience. I argue given the multiple notions of resilience, promotion of the concept requires to redefine goals and expectations in ecosystem management. The traditional view of stability, ignores the complex and natural variability of ecosystems. To operationalize resilience the challenge will be to rely on the ecosystem' adaptive capacity evolved within a changing world. Furthermore, directions for future research and implications are outlined.

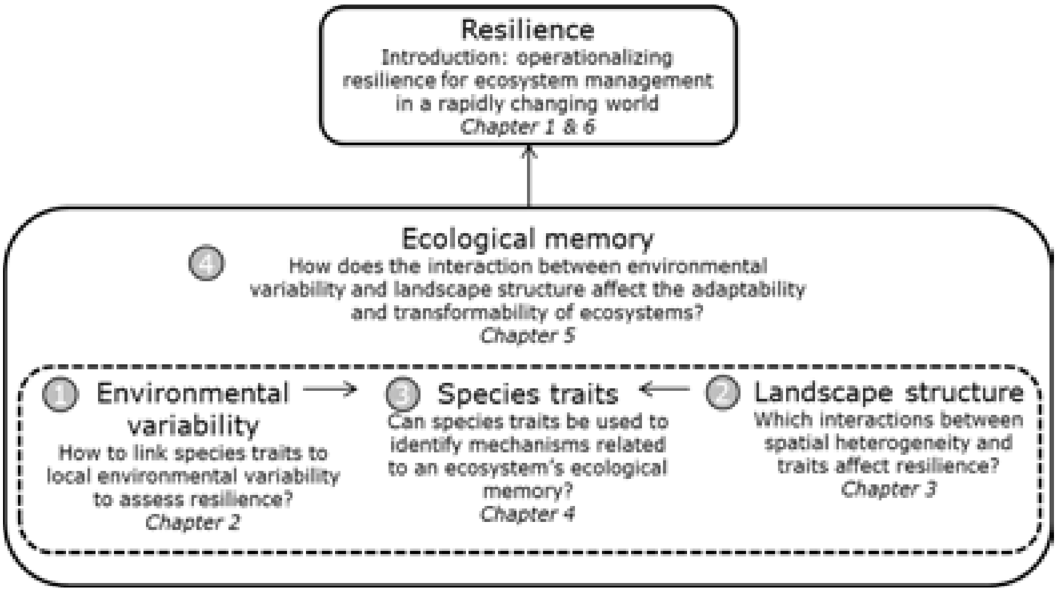

Figure 1.2. Main elements of this thesis. Numbers in circles refer to research questions

Chapter two

Assess ecosystem resilience: linking response and effect traits to environmental variability

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Abstract

Disturbances, natural as well as human, are putting constant pressure on ecosystems. These include small scale disturbances like a falling tree, but also large scale disturbances like eutrophication and climate change. Resilience is a useful indicator to assess whether an ecosystem has the capacity to maintain functioning with environmental variability. In this study we tested whether plant functional traits can be distinguished to develop a response-and-effect framework for general predictions concerning resilience. We defined response traits to assess the system's resistance to disturbance, and effect traits to assess its recovery after disturbance. We used a dataset with 932 vegetation plots containing 104 species from a selected wetland area in the Netherlands. The environmental variability was related to response traits and the response traits to effect traits with RLQ analysis, fourth-corner analysis and Spearman's rank correlation. As a result, combinations of traits that specify effects of environmental change on ecosystem resilience were found. A strong resistance to environmental variability was shown, and consequently, a positive effect on resilience. Due to correlations between response and effect traits, combinations of traits were identified having a variable effect on the resilience of the system. In this way this study argues to further develop a response-and-effect framework to understand and assess ecosystem resilience. The selection of traits is system-specific, and therefore, one should only select those response and effect traits that differentiate between response to environmental variability and effects on ecosystem functioning.

2.1 Introduction

The recent interest in ecosystem functioning has made resilience an important issue in ecosystem management and has increased awareness of the negative impacts of biodiversity loss on ecosystem functioning and long term stability (e.g., Chapin et al. 2000; Prober and Dunlop 2011; Slocum and Mendelssohn 2008; Walker 1999; Zurlini et al. 2006). Resilience indicates how well a dynamic system continues functioning in times of environmental change. Ecosystem functioning is determined by both biotic and abiotic system properties and supports processes to provide goods and services (Costanza et al. 1997; De Groot et al. 2010). Improving ecosystem resilience therefore promotes a stable supply of ecosystem services. Diaz et al. (2007) showed how an environmental factor, like land use change, can alter the functional diversity of grasslands and subsequently the provision of ecosystem services. Within the current shift of nature conservation from *species management* based on target species, to *ecosystem management* based on dynamic properties of ecosystems (Bengtsson et al. 2003; Prober and Dunlop 2011), an appropriate measure of resilience is needed (Carpenter et al. 2001). This is also requested by the Convention on Biological Diversity. However, currently no method exists on how to apply resilience in practice. Allen et al. (2011) proposed that ecosystem managers who prefer resilience can apply adaptive management to avoid that the system shifts to an alternative stable state. He describes how managers can identify the conditions that indicate loss of resilience, how they can enhance resilience and apply adaptive management to stay resilient. They assume that it is possible to identify system-specific conditions influencing resilience. Slocum and Mendelssohn (2008) assess vegetation recovery as a measure of resilience with experimental disturbances using a known stress gradient in salt marshes. However, others have argued that with increasing environmental variability (e.g., due to land use change and climate change) (Buma and Wessman 2012; McCarty 2001; Tscharntke et al. 2012), it becomes progressively difficult to predict ecosystem developments (Isbell et al. 2011) as well as the consequences for resilience (McCarty 2001). Studies from the past are insufficient with the current dimension of interacting biotic and abiotic changes. This leaves us with the challenge to operationalize the resilience concept for ecosystem management to be used in a dynamic world.

Understanding resilience in a changing environment requires a functional approach (Didham 1996) that includes ecological properties of resilience and scenarios of environmental conditions (Peters 1980). Reich et al. (2012) proposed that resilience is higher within species-rich than in species-poor communities. That is because the diversity of species responses to an environmental change allows ecosystem functioning to be maintained (Engelhardt and Ritchie 2001; Reich 2012; van der Linden et al. 2012). This is known as the insurance hypothesis (Naeem 1997; Yachi and Loreau 1999). At this functional level, species are expected to combine traits, like small but many seeds with low fecundity or canopy height that correlate allometrically with other size traits like leaf size, independent of taxonomy. These so called functional types are affected differentially by environmental variability. Knowledge about the role of functional traits can help ecosystem management (Demars et al. 2012) to focus on conditions and processes maintaining resilience. Based on the general understanding (Walker et al. 2004), we consider resilience to encompass two separate properties: 1) **resistance** - measured by the magnitude of disturbance that can be absorbed by the ecosystem without a change of functioning; and 2) **recovery** - measured by the speed of return to the original function. These two critical processes are mechanistically different and therefore require different management measures. However, they are rarely distinguished in studies concerning ecosystem functioning (France and Duffy 2006). In this study we used response traits, associated with resistance to environmental variability and effect traits which influence species recovery (Diaz and Cabido 1997). We related environmental variability with response traits and response traits with effect traits to study the system's tendency to resilience.

We adapted Suding's effect-and-response framework (Suding et al. 2008) to understand how communities interact with the environment. Environmental variability was restricted here to abiotic parameters relevant for vegetation (Figure 2.1) (Diaz et al. 1998; Tilman et al. 1996). In such a framework, abiotic parameters influence the functional trait composition of the vegetation. The shifts in species composition and the extent to which plant species differ in their traits will determine the change in resilience. With the knowledge of individual species we can extrapolate to the community level (Suding et al. 2008). Wetlands provide an ideal opportunity for such studies as they are known for their environmental gradients and they are extensively studied. Wetlands are of special importance because they provide important ecosystem services, such as water retention and purification, and are very sensitive to environmental changes.

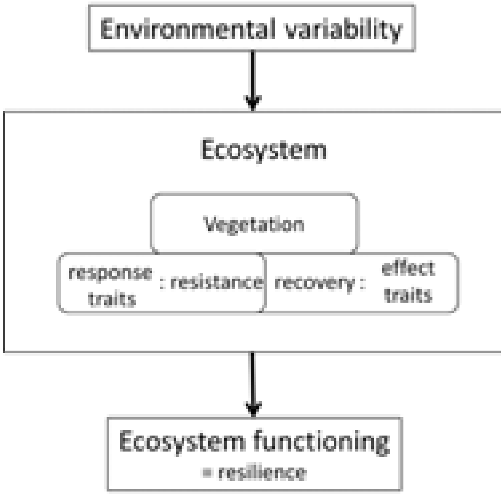

Figure 2.1. The response-and-effect framework for an ecosystem with resistance to environmental variability (the response traits) and the recovery of the vegetation (the effect traits). Resistance and recovery of the vegetation together are properties of resilience that ensures the capacity of the ecosystem to maintain functioning.

2.2 Materials and methods

Study area

Our study area is a large fen area, De Weerribben nature reserve, located in the north of the Netherlands (52°46’N; 5°56’E). It consist of 3.350 hectares of mesotrophic fens, mesotrophic and moderately eutrophic grasslands, reedlands and alluvial forests. The area is known for its gradients in hydrology, acidity and fertility, which makes it very suitable to study trait-environment relationships (Lomba et al. 2011; Runhaar et al. 1997). Nature management includes grazing, annual (late summer) mowing, and winter harvesting of reed. To maintain stable water levels, water is pumped away in wet periods and water from outside the area (i.e. allochthonous nutrient-rich water) is let in during the drier (summer) periods. Usually, this allochthonous water enters the area at one point, preferably situated in one of the larger lakes. Consequently, in remote and hydrologically isolated places the water quality is less influenced by external factors (Geurts et al. 2010).

Vegetation data

We used abundance data of 932 vegetation plots (each 1x1 km) (Hennekens and Schaminee 2001; Ozinga 2008). Data were collected between 1990 and 2006. From the 232 recorded plant species we excluded: [1] mosses, ferns and orchids, as there is little known about their trait values; [2] trees, as for many species their abundance is influenced by afforestation; and [3] aquatic species, as they are related to different environmental factors than terrestrial species and in general occur marginally (Ozinga 2008). Furthermore, we excluded species with less than four records per trait value to minimize effects of measurement errors. Finally, we only included species that were present in at least 1% of the 932 plots, to avoid bias due to sporadically or randomly occurring species. The selected species are likely associated with the dominant environmental gradients and therefore useful for our framework (Cao et al. 2001). The final data set comprises 104 suitable plant species that can be found in Appendix 2.1.

Environmental data

To characterize the relevant aspects of the environment we used seven abiotic parameters (Table 2.1). The species indicator values, based on a large dataset of vegetation records paired by soil chemical data (Wamelink et al. 2005; Wamelink 2012) were used to estimate these abiotic parameters by averaging per plot the species’ indicator values (using unweighted means, i.e. abundance values for the species were not used as it made no difference in the results). Table 2.1 shows this study’s abiotic parameters, resembling main environmental gradients in our wetland system.

Table 2.1. Abiotic parameters used in the analysis and the range of values calculated for the study area.

Abiotic parameter	Acronyms	Type of variable	Range of values
Amplitude of groundwater level*	AG	Continuous (cm)	54.8 – 64.9
Soil acidity	pH (H_2O)	Continuous	3.9 – 6.7
Calcium content of the soil (in water extract)	Ca	Continuous (mg/kg)	3352.7 – 6607.6
Chloride content of the soil (in water extract)	Cl	Continuous (mg/kg)	87.8 – 151.0
Nitrate content of the soil (in a CaCl2 extract)	NO_3	Continuous (mg/kg)	7.4 – 39.8
Total Phosphorus of the soil	Ptot	Continuous (mg/kg)	598.2 – 784.8
Moisture content of the soil	Moisture	Continuous (%)	20.0 – 32.8

* The amplitude is calculated as the difference in lowest ('dry', summer) and highest ('wet', winter) groundwater level.

Response and effect traits

To understand the mechanisms of resilience with environmental variability we selected five response traits, which are good predictors of species resistance to environmental variability, and five effect traits with an effect on recovery (Table 2.2). Separating response and effect traits enables us to define the mechanisms of resistance and recovery and the strength of the relationship between the two processes. That defines the resilience of the system. Trait values such as low Specific Leaf Area (SLA), occurrence of below ground perennial buds, large canopy height, small leaves and occurrence of aerenchyma are associated with increase in resistance (Cornelissen et al. 2003; Kleyer et al. 2008; vanGroenendael et al. 1996), whereas clonal growth, long distance dispersal, large lateral spread, long seed longevity and high seed mass are important for rapid recovery (Ehrlen and Eriksson 2000; McConkey et al. 2012). Trait values were obtained from different databases, ranked below in order of importance: 1) LEDA Traitbase (Kleyer et al. 2008); 2) Clo-Pla3 – database of clonal growth of plants from Central Europe (Klimešová and Klimeš, 2008; Klimesova and de Bello 2009); 3) field data; 4) second-hand information; 5) picture interpretation; and 6) expert knowledge (pers.comm. W.A. Ozinga and A. Klimkowska) as a last choice. We included only those traits with a minimum of four measurements and calculated the average value.

Table 2.2. Response and effect traits with their classes used in the analyses.

	Response traits	Acronyms	Type of variable	Classes	Literature
1	Specific Leaf Area	SLA	Continuous	Quantitative (mm^2)^a	Kleyer et al. (2008)
2	Growth form	GF	Nominal	Perennial buds: 1= above ground 2= below ground	Kleyer et al. (2008)
3	Canopy height	CH	Continuous	Quantitative (m)^a	Poschlod et al. (2003), Fitter and Peat (1994)
4	Leaf size	LS	Continuous	Quantitative (mm^2)^a	Poschlod et al. (2003); Klotz et al. (2002); Kleyer et al. (2008) ; expert knowledge
5	Aerenchyma	AC	Nominal	1=yes 2=no	Kleyer et al. (2008)
	Effect traits				
6	Clonal growth	CG	Nominal	1=yes 2=no	Klimešová and Klimeš; Klimešová and de Bello
7	Dispersal mode	DM	Ordinal	0=short distance^b 1=long distance^b	Bouman et al. (2000); Royal Botanic Gardens Kew (2008)
8	Lateral spread	LS	Ordinal	1= 0 (m) 2= <0.01 (m) 3= <0.25 (m) 4= >0.25 (m)	Klimešová and Klimeš; Klimešová and de Bello; Kleyer et al. (2008)
9	Seed longevity	SL	Ordinal	1=transient 2=short term 3=long term	Klotz et al. (2002)
10	Seed mass	SM	Continuous	Quantitative (g)	Royal Botanic Gardens Kew (2008)

[a]trait log-10 transformed for analyses; [b]short distance includes bird feed, ants, spilling short distance (incl. rainwater). Long distance includes water, wind, mammalian dung, mammalian fur, bird droppings.

Statistical analysis

To determine the relationships between abiotic parameters and response traits, incorporating species abundance, we conducted a three-table RLQ and fourth-corner analysis (Dray and Legendre 2008). We created three tables **R**, **L** and **Q** with the values of seven abiotic parameters in the 932 plots, the abundance of 104 species in the 932 plots, and the values of five response traits of the 104 species, respectively. The analysis explores the joint structure among these three tables. The **L** table serves as a link between the **R** table and **Q** table, and measures the strength of the relationship between them. First we analysed each table separately, to be able to compare the results with the RLQ analysis. The **L** table, using ln(*y*+1) transformed abundances, was analysed by a correspondence analysis (Warren et al. 2001). We conducted principal component analysis (PCA) on the **R** table and **Q** table. To relate the abiotic parameters to the response traits, the RLQ analysis performed a co-inertia analysis on the cross-matrix of **R**, **L** and **Q**. This analysis seeks to maximize the covariation between abiotic parameters (R) and response traits (Q). As a result, the best joint combination of the ordinations of plots constrained by their abiotic parameters, the ordination of species constrained by their response traits, and the synchronous ordination of species and plots is calculated (Ribera et al. 2001). There are several null models to assess the significance of pairwise relationships between abiotic parameters and response traits in the fourth-corner analysis. We followed the suggestion of Dray and Legendre (2008) and used the 'two-step approach' which combines the results of 1000 permutations of Model 2 and 4 to obtain significance of the relationships. All calculations were done using the ade4 - package (Dray and Dufour 2007). Finally we calculated Spearman rank correlation coefficients to quantify and test the strength of the relationship between response and effect traits.

2.3 Results

The RLQ analysis revealed significant association between abiotic parameters and response traits ($P < 0.001$, based on a permutation test for the total coinertia). From the correspondence analysis of the **L** table a canonical correlation of 0.85 was found, indicating that the **L** table has potential to link abiotic parameters (R) to response traits (Q). In the PCA of the abiotic parameters, the first two axes explained 55% and 19% of the total abiotic variance. For the response traits these percentages were 46% and 22% respectively. In the RLQ analysis, 82% of the abiotic variance, as captured by the PCA, was explained by the first two RLQ axes (Table 2.3). For the response traits 85% of the variance captured by the PCA was explained by the first two RLQ axes (Table 2.3). These results indicate that the RLQ analysis was able to link substantial portions of variation of abiotic parameters to response traits through the plant abundances.

Table 2.3. Results of the RLQ analysis of response traits.

RLQ axes	Axis 1	Axis 2
Eigenvalues	0.346	0.040
Covariance	0.588	0.199
Correlation	0.229	0.211
R: RLQ/PCA	78%	82%
L: RLQ/COA	27%	31%
Q: RLQ/PCA	94%	85%

R: RLQ/PCA represents the percentage of the variance of the separate analysis of table R (abiotic parameters x vegetation plots) accounted for by each of the first two ordination axes of the RLQ analyses. L: RLQ/COA is the same for the separate analysis of table L (vegetation plots x species) and Q: RLQ/PCA is the same for the separate analysis of table Q (traits x species). It is calculated as the ratio of the axis eigenvalue of RLQ analysis on the corresponding axis eigenvalue of separate analysis.

The abiotic parameters that showed the highest (positive) correlation with the first axis of the RLQ analysis, were chloride, nitrate and phosphorus content; pH showed a negative correlation (Figure 2.2). The same axis loaded also positively on moisture, and negatively on groundwater amplitude. Therefore, the main environmental gradient, strongest related to plant response traits, stretches from nutrient-rich, high moisture and low pH environments to nutrient-poor, low moisture, high pH areas with high groundwater amplitude. The response trait with the highest (positive) correlation with the first axis was canopy height, but high positive loadings were also found for leaf size and occurrence of below ground perennial buds. Meaning that the lower pH, higher nutrient contents and higher chloride content were related with higher canopy height, larger leaf size, and more frequent occurrence of perennial buds below ground. SLA correlated negatively with this axis (Figure 2.2). For the abiotic parameters, the second RLQ axis had highest correlation with pH; smaller contributions were found for nitrate and phosphorus content. The response trait loading highest on this second axis was SLA, with leaf size and aerenchyma coming second. Hence, higher pH was related to higher SLA and less presence of aerenchyma. The ordination of species completes the RLQ results (Appendix 2.2). Traits associated with herbaceous vegetation of fen-meadows, such as relatively small specific leaf area, presence of aerenchyma and small canopy height were located towards the centre of the diagram, indicating that they were shared by species on a terrestrial-aquatic transition zone.

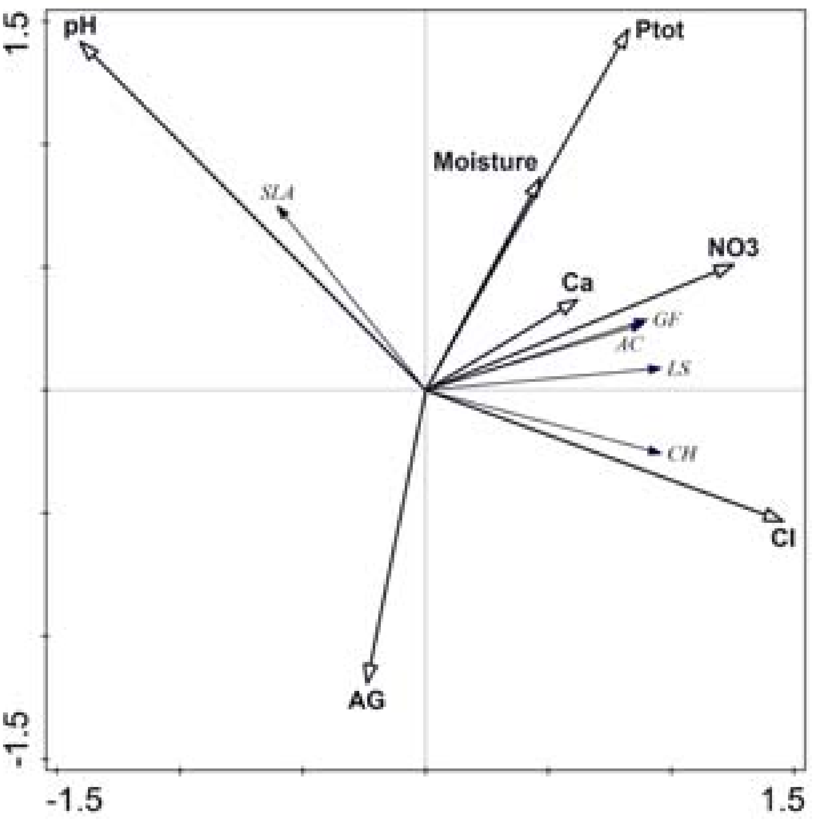

Figure 2.2. RLQ biplot showing the relationships of abiotic parameters and response traits. See Table 2.1 and 2.2 for key to acronyms.

The fourth-corner analysis revealed several significant associations, in line with the findings from the RLQ analysis. Strongest associations ($P<0.01$) were found between the nutrients nitrate / chloride on one side, and canopy height / leaf size on the other, and between phosphorus and below ground perennial buds (Table 2.4).

Table 2.4. Results from fourth-corner analysis on resistance using 104 plant species. Numbers indicate P-values of relationships between pairs of response traits and abiotic parameters (acronyms as in Tables 2.1 and 2.2).

	AG	pH	Ca	Cl	NO_3	Ptot	Moisture
SLA	n.s.	0.041+	n.s.	0.017-	n.s.	n.s.	n.s.
GF	n.s.	n.s.	n.s.	0.025+	0.040+	0.008+	n.s.
CH	n.s.	n.s.	0.024+	0.002+	0.001+	0.013+	0.031+
LS	n.s.	n.s.	n.s.	0.010+	0.002+	0.024+	n.s.
AC	0.048-	n.s.	n.s.	n.s.	n.s.	n.s.	0.034+

Plus and minus signs indicate the direction of significant relationships; n.s., non-significant relationship.

Spearman rank correlation between response and effect traits

The Spearman rank correlation tests between response and effect traits within our dataset showed the most significant positive correlation between leaf size and seed mass, and negative correlation between aerenchyma and seed longevity ($p < 0.001$). Less significant was the positive correlation between canopy height and lateral spread ($p < 0.01$) and growth form and clonal growth ($p < 0.05$).

2.4 Discussion and conclusions

In this study we have applied several analyses to relate environmental variability with response and effect traits relevant to the two components of resilience (i.e. resistance and recovery). Especially the RLQ and fourth-corner analyses reflected how abiotic parameters influence the functional trait composition of the vegetation. From the shifts in response and effect traits we can determine the change in resilience.

Abiotic parameters and response traits

The vegetation showed a pattern in the distribution of response traits on the main environmental gradients characteristic for wetlands. Our results are in agreement with other studies (e.g., Ordonez et al. 2009; van Bodegom et al. 2006). In this study the filtering of species is driven more strongly by N- and P-availability, chloride content and pH than by hydrology. However, the N- and P- availability as well as chloride content and pH are affected by hydrology; thus, hydrology is still an important, indirect driver of the functional characteristics of the vegetation. This partly comes from the supply of allochthonous water during drier (summer) periods for the strict control of hydrological variability that is currently applied in the area (stabilised water levels) and from an effect of water quality (rainwater, slightly alkaline surface water and base-rich groundwater) on nutrient availability and pH conditions. The combination of large groundwater amplitude and low moisture is a property of isolated places caused by natural processes typical for fen areas. The groundwater under De Weerribben comprises local pockets of brackish water which cause the strong positive relation of chloride content with the first RLQ axis (Wirdum 1991). Higher nutrient availability and low pH conditions selected for species with high resistance.

The first two ordination axes of RLQ analysis accounted for a large fraction of the explained variance for the abiotic parameters and the species traits, indicating that environmental gradients structure vegetation and the trait composition of occurring species. The individual traits mostly associated with the first RLQ axis were canopy height, growth form and aerenchyma. The second RLQ axis was mostly associated with SLA and growth form. These results show that conditions of relatively high nutrient content and low pH tend to select for species with higher canopy, growth form with below-ground perennial buds, aerenchyma and relative small SLA. This functional characteristics point to a strong resistance to environmental variability and, consequently, a positive effect on resilience.

Link between response and effect traits

Testing the relation between response and effect traits showed a negative relation between aerenchyma and seed longevity. A transient seed longevity will have a negative effect on recovery and in consequence negative effect on resilience. Positive relations are found between leaf size and seed mass, canopy height and lateral spread, and growth form with perennial buds below ground and clonal growth. In general we found that if nutrient availability and chloride content increase (i.e. more water input from outside of the area, less water fluctuation), then larger plants with below ground perennial buds and large SLA will take over and consequently plants with high lateral spread, clonal growth and large seeds increase. These plants are probably successful if they have to germinate and grow in a thick, productive vegetation – but are less successful with long distance dispersal. As a consequence, the persistence as well as the recovery will increase and therefore the resilience of the system will increase. However, the recovery takes place on a relative short distance compared to plants with small seeds. The results confirm the model of Bossuyt and Honnay (2006) who also found that a response trait like plant life span had a strong positive effect on persistence, irrespective of the plant's effect traits dispersal capacity and population growth rate. Plant species that invest in persistence require less investment in recovery even with environmental variability.

Response-and-effect framework as a tool for management

Using species traits to construct a response-and-effect framework is a promising method to understand ecosystem resilience. It allows the user to define response traits associated with resistance and effect traits associated with recovery. Furthermore, it enables one to define relationships between response and effect traits. Moreover, this framework provides a mechanistic understanding of resilience based on environmental variables and species abundance. Although we could not fully quantify ecosystem resilience with the used traits, we clearly showed that there is a relationship between abiotic parameters and response traits. The correlation between response and effect traits supports our aim to define the change in resilience with environmental variability.

In this study we combined local plant species data with abiotic parameters calculated for the Netherlands as a whole and trait values collected in North-West Europe. Previous studies showed that plant traits in various types of ecosystems can be generalized (e.g., Cornelissen et al. 2003; Diaz et al. 2004). However, our results do not fully confirm these studies, as we did not find all expected relationships among environment, response and effect traits. The power of our response-and-effect framework seems to be limited by the identification of relevant traits to be used on the ecosystem level and lack of trait information (van der Linden et al.

2012). It is for that reason that Wesuls et al. (2012) suggest partitioning environmental variation to allow control for the effects of different environmental filters at various scales. This is especially applicable in highly variable environments, as in this study of wetlands. However, the environmental complexity of their study is much higher than we needed for our study. With our response-and-effect framework, we assumed that resilience is the result of independent traits – while in reality they are not. The underlying assumption is that with changing environmental variables the species' responses and effects do not depend on the abundance of other species. The result is a predictable change in resilience based on the sum of independent response and effect traits. However, other studies propose non-additive effects as an alternative ecological mechanism (Suding et al. 2008), which refer to the context-specific species interaction, depending on the identity and traits of other species. To adopt the non-additive effect in the framework complicates the development while the added value to our understanding of resilience is uncertain. In this context, we recommend to detect system-specific response and effect traits in highly variable ecosystems.

In conclusion, we demonstrated here that such a response-and-effect framework for ecosystem resilience can be a useful tool for ecosystem management to define goals focusing on adaptation in changing environments. In this study area, abiotic parameters related to pH, chloride and nutrients have more effect on the combinations of response and effect traits than hydrology. Our results show that measures to regulate (some) abiotic parameters are likely to influence the resilience. However, every system also has its own confounding environmental factors (e.g., fragmentation, heterogeneity, light, climate change) interacting with ecosystem processes, and complexity increases the uncertainty about system responses on different spatial scales (Keith et al. 2011; Tscharntke et al. 2012; Zurlini et al. 2006). These system dynamics seek for adaptive management with explicit definition of management goals to maintain ecosystem functioning, as the adaptive approach makes management more robust with environmental variability.

Appendix 2.1

Table. A.2.1 Plant species with their codes included in the study.

	Species	Codes
1	Agrostis_canina	Agr_can
2	Agrostis_capillaris	Agr_cap
3	Agrostis_stolonifera	Agr_sto
4	Alopecurus_geniculatus	Alo_gen
5	Angelica_sylvestris	Ang_syl
6	Anthoxanthum_odoratum	Ant_odo
7	Bellis_perennis	Bel_per
8	Bromus_hordeaceus	Bro_hor
9	Caltha_palustris	Cal_pal
10	Calystegia_sepium	Cal_sep
11	Cardamine_pratensis	Car_pra
12	Carex_acuta	Car_acu
13	Carex_acutiformis	Car_acf
14	Carex_disticha	Car_dis
15	Carex_echinata	Car_ech
16	Carex_elata	Car_ela
17	Carex_nigra	Car_nig
18	Carex_panicea	Car_pa
19	Carex_paniculata	Car_pan
20	Carex_pseudocyperus	Car_pse
21	Carex_riparia	Car_rip
22	Carex_rostrata	Car_ros
23	Cerastium_fontanum	Cer_fon
24	Cicuta_virosa	Cic_vir
25	Cirsium_palustre	Cir_pal
26	Cladium_mariscus	Cla_mar
27	Drosera_rotundifolia	Dro_rot
28	Elytrigia_repens	Ely_rep
29	Epilobium_hirsutum	Epi_hir
30	Epilobium_palustre	Epi_pal
31	Equisetum_fluviatile	Equ_flu
32	Erica_tetralix	Eri_tet
33	Eriophorum_angustifolium	Eri_ang
34	Eupatorium_cannabinum	Eup_can
35	Euphorbia_palustris	Eup_pal
36	Festuca_pratensis	Fes_pra
37	Festuca_rubra	Fes_rub
38	Filipendula_ulmaria	Fil_ulm
39	Galeopsis_tetrahit	Gal_tet
40	Galium_palustre	Gal_pal
41	Galium_uliginosum	Gal_uli
42	Glechoma_hederacea	Gle_hed
43	Glyceria_fluitans	Gly_flu
44	Glyceria_maxima	Gly_max
45	Hierochloe_odorata	Hie_odo
46	Holcus_lanatus	Hol_lan
47	Hydrocotyle_vulgaris	Hyd_vul
48	Iris_pseudacorus	Iri_pse
49	Juncus_articulatus	Jun_art
50	Juncus_conglomeratus	Jun_con
51	Juncus_effusus	Jun_eff
52	Juncus_subnodulosus	Jun_sub
53	Lathyrus_palustris	Lat_pal
54	Leontodon_autumnalis	Leo_aut

55	Lolium_perenne	Lol_per
56	Lotus_pedunculatus	Lot_ped
57	Luzula_multiflora	Luz_mul
58	Lychnis_flos-cuculi	Lyc_flo
59	Lycopus_europaeus	Lyc_eur
60	Lysimachia_nummularia	Lys_num
61	Lysimachia_thyrsiflora	Lys_thy
62	Lysimachia_vulgaris	Lys_vul
63	Lythrum_salicaria	Lyt_sal
64	Mentha_aquatica	Men_aqu
65	Menyanthes_trifoliata	Men_tri
66	Molinia_caerulea	Mol_cae
67	Myrica_gale	Myr_gal
68	Polygonum_maculosa	Pol_mac
69	Peucedanum_palustre	Peu_pal
70	Phalaris_arundinacea	Pha_aru
71	Phragmites_australis	Phr_aus
72	Plantago_lanceolata	Pla_lan
73	Plantago_major	Pla_maj
74	Poa_annua	Poa_ann
75	Poa_palustris	Poa_pal
76	Poa_pratensis	Poa_pra
77	Poa_trivialis	Poa_tri
78	Potentilla_erecta	Pot_ere
79	Potentilla_palustris	Pot_pal
80	Ranunculus_acris	Ran_acr
81	Ranunculus_flammula	Ran_fla
82	Ranunculus_lingua	Ran_lin
83	Ranunculus_repens	Ran_rep
84	Ranunculus_sceleratus	Ran_sce
85	Rubus_fruticosus	Rub_fru
86	Rumex_acetosa	Rum_ace
87	Rumex_hydrolapathum	Rum_hyd
88	Salix_repens	Sal_rep
89	Scutellaria_galericulata	Scu_gal
90	Senecio_aquaticus	Sen_aqua
91	Sium_latifolium	Siu_lat
92	Solanum_dulcamara	Sol_dul
93	Stachys_palustris	Sta_pal
94	Stellaria_media	Ste_med
95	Stellaria_palustris	Ste_pal
96	Symphytum_officinale	Sym_off
97	Thalictrum_flavum	Tha_fla
98	Trifolium_repens	Tri_rep
99	Typha_angustifolia	Typ_ang
100	Typha_latifolia	Typ_lat
101	Urtica_dioica	Urt_dio
102	Valeriana_dioica	Val_dio
103	Valeriana_officinalis	Val_off
104	Viola_palustris	Vio_pal

Appendix 2.2

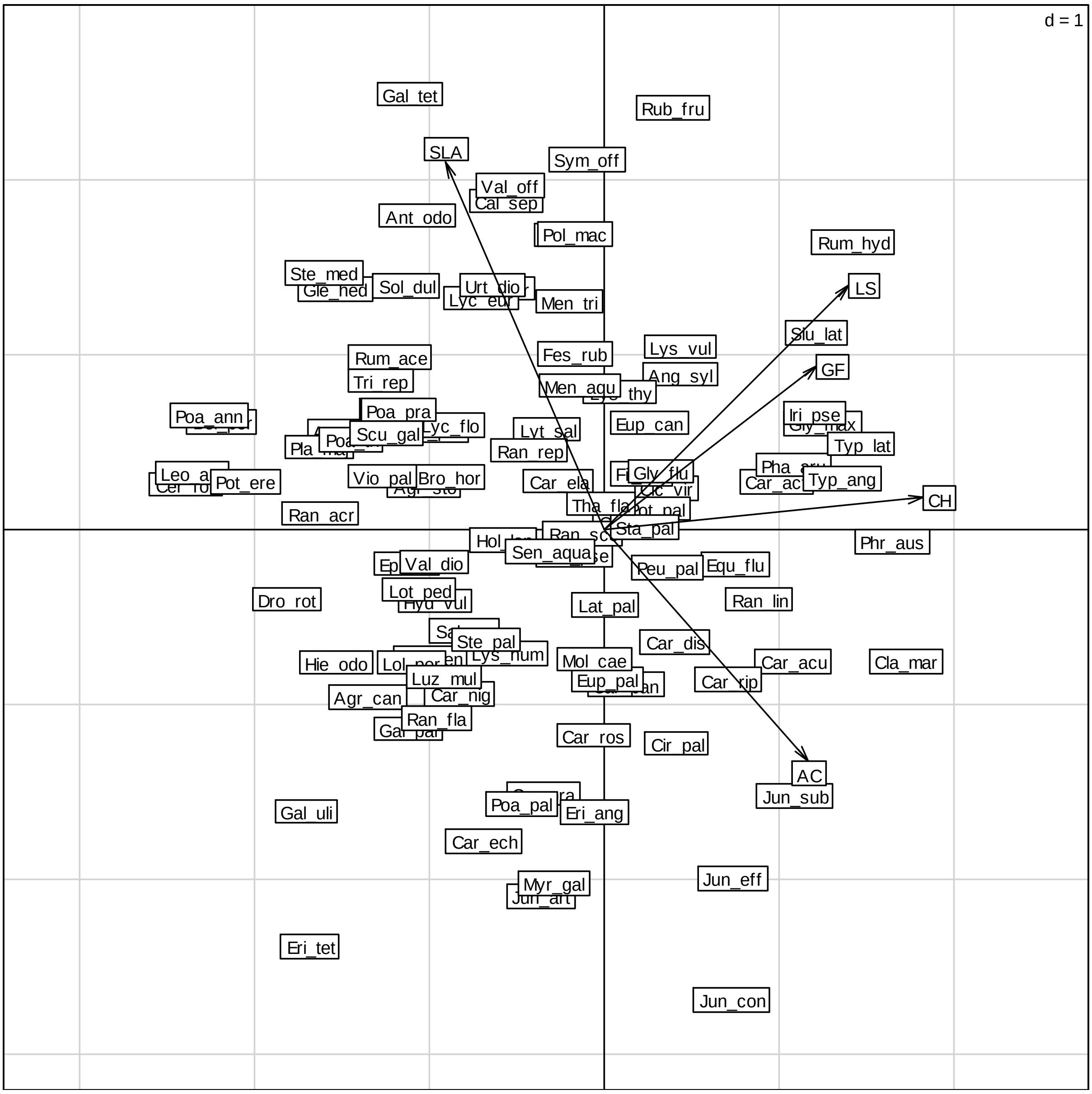

Figure. A.2.2. Graphical display of RLQ scores of plant species and response traits. See Appendix 2.1 for the names of plant species and Table 2.1 for key to acronyms of response traits.

Chapter three

Towards resilience-based ecosystem management: linking spatial heterogeneity to species traits of plants and butterflies

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Abstract

With environmental change, managing for resilience is essential to maintain ecological functioning. Trait-based approaches in the analysis of species assemblages are helpful to understand possible links between species composition and the adaptive capacity of the ecosystem. According to Tscharntke's 'landscape-moderated functional trait selection hypothesis', environmental changes affect species traits differently. Inspired by this hypothesis we analysed the relationship between spatial heterogeneity and trait composition for butterflies and vascular plants. Focussing on wetlands in the Netherlands, we disentangled the relation between spatial heterogeneity at increasing spatial extents (1, 2 and 5 km radius) and traits related to the resistance and recovery of 19 butterfly species and 120 plant species using RLQ and Fourth Corner analyses. The results show that heterogeneity indices and spatial extent affect trait composition for both species. The total length of linear elements in the landscape (e.g., ditches and hedgerows) and the diversity of wetland types were related to butterfly traits. The aggregation and diversity of land cover related most to plant traits. However, we found no indication that the scale at which heterogeneity affects trait composition differed between the two species groups. The approach adopted in this study yielded insights into the effects of spatial heterogeneity on trait composition for the species of interest, thereby highlighting the importance of considering the extent of spatial heterogeneity and the effect this may have on ecological resilience.

3.1 Introduction

Resilience is increasingly acknowledged as an important concept in facing environmental change (Scheffer et al. 1993; Peterson et al. 1998; Sundstrom et al. 2012). Ecological resilience indicates the magnitude of disturbance that can be absorbed before an ecosystem redefines its structure by changing both biotic and abiotic properties, also referred to as adaptive capacity (Gunderson 2000). Given the present variety of human and natural impacts like land-use change, eutrophication and climate change, we cannot take this capacity for renewal and reorganization for granted (Chapin et al. 2000). A focus on two properties of the adaptive capacity, namely (i) species' resistance to disturbance and (ii) species' recovery after disturbance, provides insight into the processes that structure communities across scales, and the impact that species have on ecosystem functioning (Peterson et al. 1998; Lavorel and Garnier, 2002; Diaz et al. 2007; Sterk et al. 2013).

Although the potential of the concept of ecological resilience is intensively discussed, a coherent ecosystem management to enhance ecological resilience is still lacking. Identifying how we can maintain and enhance the adaptive capacity can be of great value to managers facing environmental change. Nowadays, landscapes are a mix of natural environments and human land uses, developed across environmental gradients. Species experience a landscape as suitable habitat and non-suitable habitat patches at species-specific extents (Murphy and Lovett-Doust 2004; Kumar et al. 2009). Accumulating evidence shows that landscape structure is related to ecological resilience (Opdam et al. 2006; Verboom et al. 2010; Schippers et al. 2015; Campbell et al., 2015), however, the significance of ecosystem processes at different spatial scales is often neglected. Spatial heterogeneity results from spatial interactions between biotic and abiotic factors driving biodiversity (Wiens 1976; Kumar et al. 2006). There are many examples in landscape ecology how spatial heterogeneity influences ecosystems at both local and landscape scale (Kumar et al. 2006; Fahrig et al. 2011; Turner et al. 2013). Most research shows a positive effect of heterogeneity on, for instance, population stability (Oliver et al. 2010; Oliver et al. 2014), dispersal (Abd El-Ghani et al. 2011; Atauri and de Lucio 2001; Marini et al. 2010) and population survival (Piha et al. 2007; Kumar et al. 2009). However, the methods used are not suitable to disentangle the mechanisms incorporating resistance and recovery. We propose a trait-based approach to identify how spatial heterogeneity selects for trait values contributing to ecological resilience (Lundberg and Moberg 2003).

Several attempts to operationalize ecological resilience are available and most are based on species traits (Lavorel and Garnier 2002; Pausas et al. 2004). Species traits provide better insight in changing species composition as a response to environmental variation and the effects on ecosystem functioning than species identity alone (e.g., Elmqvist et al. 2003; Shipley et al. 2006; de Bello et al. 2010; Douma et al. 2012; Van Bodegom et al. 2012).

Examples like a trait frequency analysis of the earthworm community in river flood plains showed a positive association between trait diversity and resilience to flooding (De Lange et al. 2012). Sterk et al. (2013) used a ‘response-and-effect framework’ to assess ecological resilience of wetland vegetation. They distinguished between a species’ response to disturbance and the effect on ecosystem functioning. As such, a trait-based approach could help a manager to predict how decisions associated with landscape change might impact communities or specific species of conservation concern.

Species traits are related to ecological processes acting across scales with different levels of heterogeneity (Peterson et al. 1998; de Blois et al. 2002; Oliver et al. 2010; Weaver et al. 2012). For example, when landscapes change due to homogenization, a multi-scale selection of functionally important traits is taking place, influencing the community’s functional roles (Tscharntke et al. 2012). Taking the interaction between spatial heterogeneity and the abundance of traits a step further, Tscharntke et al. (2012) hypothesized that the landscape itself can select for specific traits, which would have clear effects on ecological resilience in time and space (Turner 1989; Laliberte et al. 2010; Bagaria et al. 2012; Willis et al. 2012; Pasher et al. 2013). However, these studies do not provide concrete policy or management measures or address how to maintain or enhance the resilience of ecosystems. The question remains whether there is a consistent relationship between spatial heterogeneity across scales and traits that capture species’ ability to resist and recover with disturbances.

So far, the consequences of spatial heterogeneity for ecosystem functioning have rarely been studied. In this study, inspired by Tscharntke et al.’s (2012) hypothesis, we analyze the relationship between spatial heterogeneity and trait composition at increasing spatial extents (1, 2 and 5 km radius) for wetland butterflies and vascular plants. The traits selected in this study are related to the adaptive capacity of the system as they have a function in the resistance or recovery of species regarding disturbance of ecosystems (Sterk et al. 2013). Some traits are related to the landscape configuration, like dispersal mode of plants (e.g., capacity for long-distance dispersal by wind or water) in relation to fragmentation (Ozinga et al. 2005; Tremlova and Münzbergová 2007; Ozinga et al. 2009). Other traits result from habitat requirements, like moisture range and the presence of aerenchyma (Vandewalle et al. 2013; Ozinga et al. 2013). Our aim is to identify (1) if heterogeneity selects for specific traits, (2) at which spatial extent the heterogeneity relates best to traits, and (3) how are land cover types related to the selected traits.

Butterflies and plants differ in their life-history, trophic levels and dispersal strategies and follow very different strategies to cope with disturbances (e.g., Reich et al. 2003). Heterogeneity can influence the performance of specific strategies through different, but not mutually exclusive mechanisms (see, for example, Ockinger et al. 2012). Because of the involvement of different processes, we hypothesize that the landscape extent for which heterogeneity best predicts species traits differs within and between species groups, with plants responding at smaller spatial extent and butterflies at larger spatial extent. This study provides a better understanding how spatial heterogeneity selects species traits across multiple spatial extents.

3.2 Materials and methods

Study area

In our study, we focus on wetlands ranging from marshlands in the west of the Netherlands to bogs in the east of the Netherlands. We selected sixteen wetlands for butterflies and thirteen wetlands for plants (Figure 3.1). Our selection is based on ample available abundance data for both taxonomic groups in these wetlands (Dutch Butterfly Monitoring Scheme (van Swaay et al. 2002); Dutch National Vegetation Database (Schaminée et al. 2012)).

Figure 3.1. Maps of the Netherlands with the locations of the studied wetlands (circles). Area's used to monitor butterflies on the left map and areas used to monitor plants on the right map. Codes refer to Appendix 3.3.

The abundance of each butterfly species is calculated from monitoring data for the period 2000-2010 with records from at least five years. We excluded species that were present in only one wetland as well as wide-ranging species which do not show a specific dependence on wetlands in terms of distribution records or greater abundance on monitoring transects. This avoids bias due to sporadically or randomly occurring species. The final data set comprises 19 suitable butterfly species (Appendix 3.1). Plant presence data are derived from vegetation plots (at least 25 plots from 16-100m^2 within each 1x1 km grid-cells) (Schaminée et al. 2007; Schaminée et al. 2012) (Figure 3.1). Data were collected between 1990 and 2006. From the recorded plant species we excluded (1) mosses, ferns and orchids, as their trait values are largely unknown, (2) trees, as their abundance is influenced by afforestation, and (3) aquatic species, which are related to different environmental factors than terrestrial species (Ozinga 2005). The final data set comprises 120 plant species (Appendix 3.2).

Heterogeneity indices

Spatial heterogeneity is defined as spatial discontinuity in ecological relevant characteristics and contains three aspects: (1) the *diversity* of land cover types, (2) the *configuration* of land cover types, (3) the *configuration* of landscape elements. The study is focused on wetland types (hereafter referred to as “habitat”), but we also incorporated other land cover types together with the wetland types in the analyses (hereafter referred to as “landscape”). To quantify heterogeneity metrics within and around the study areas we used FRAGSTATS (McGarigal and Marks 1994) (Table 3.1).

Table 3.1. Heterogeneity metrics used to test the relation between spatial heterogeneity and traits at increasing spatial extents (1, 2 and 5 km radius).

Indices	Description
Contagion *L'* index	Extent to which landscape types are aggregated or clumped as a percentage of the maximum possible. Types are: water, reedland, wet forests, natural grassland, pasture grazing land, agriculture, deciduous forest, pine forest, heather/sand, urban area and arable land.
Shannon-Wiener *L'* Index	Quantifies the diversity of landscape types based on two components: the number of different types and the proportional area distribution among types. Types are: water, reedland, wet forests, natural grassland, grazing land, agriculture, deciduous forest, pine forest, heather/sand, urban area and undefined.
Hedgerows	Total length of hedgerows per radius.
Ditches	Total length of ditches per radius.
Contagion *H'* index	Extent to which habitat types are aggregated or clumped as a percentage of the maximum possible. Types are: water, reedland, wet forests, natural grassland and others.
Shannon-Wiener *H'* Index	The Shannon Diversity Index quantifies the diversity of habitats based on two components: the number of different habitats and the proportional area distribution among types. Types are water, reedland, wet forests, natural grassland and others.

We calculated diversity using the Shannon-Wiener Index, which accounts for relative abundance and the number of habitat types (indicated with ‘*H*) and landscape types (indicated with ‘*L*) within a study area. The Shannon-Wiener *H'* Index was classified into six habitat types suitable for the species (Table 3.1) using remotely sensed data from Top10NL (TOP10-SE, 2006). We also calculated the Shannon-Wiener *L'* Index of the landscape with thirteen types (Table 3.1) using the same remotely sensed data. A higher value for the Shannon-Wiener Index refers to higher heterogeneity (Figure 3.2). The contagion *H'* index was used to calculate the configuration of the six habitat types and the contagion *L'* index was used to calculate the configuration of the thirteen landscape types (Table 3.1). A lower contagion index refers to higher heterogeneity (Figure 3.2). Also abundant linear landscape elements increase heterogeneity (Lindborg et al. 2014). Especially in cultural landscapes linear elements, like hedgerows or ditches, contribute to the variation in micro-climate from open to closed vegetation along hedgerows, and wet to dry conditions along ditches. Linear elements also increase connectivity in fragmented areas (Grashof et al. 2009). We calculated this heterogeneity metrics as the total length of ditches and hedgerows per spatial extent.

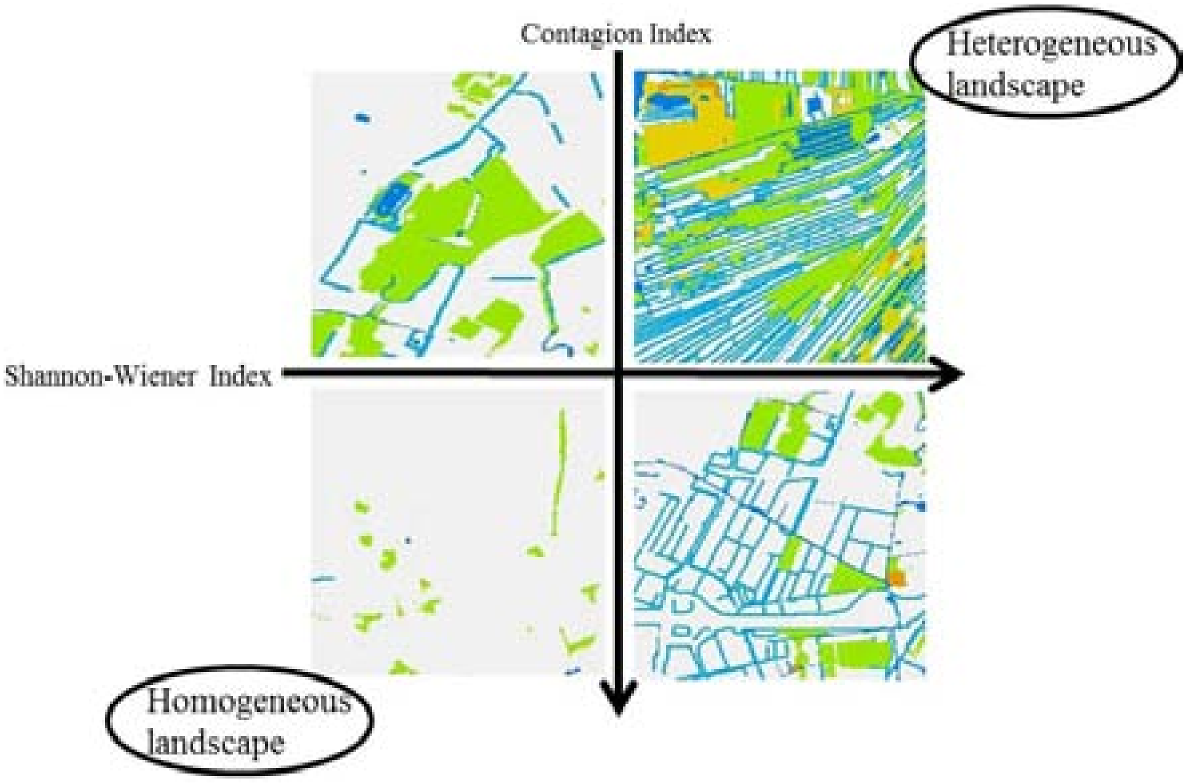

Figure 3.2. Maps of landscapes showing the effects of different heterogeneity metrics. A high Shannon-Wiener Index and a low Contagion Index results in a heterogeneous landscape with a high landscape diversity and low aggregation. A low Shannon-Wiener Index and a high Contagion Index results in a homogeneous landscape with a low landscape diversity and high aggregation.

Effects of heterogeneity on species are often found to be strongest at a specific extent surrounding the study area where species are sampled (Pasher et al. 2013; Alignier et al. 2013; Steckel et al. 2014). Therefore, analyses are conducted at multiple extents to determine the scale of the effect. The heterogeneity metrics are calculated over three spatial extents reflecting areas where management can influence heterogeneity and at which an influence of heterogeneity on the organisms can be expected: 1, 2 and 5 km radius around the middle of the transect (butterflies) or the plots (plants). The centroid of these extents is always located in a wetland (see example in Appendix 3.4). This implies that spatial heterogeneity in smaller extents is more associated with habitat types calculated with the Shannon-Wiener *H'* Index, while larger extents reflect heterogeneity of the landscape types calculated with the Shannon-Wiener *L'* Index. Detailed information per radius can be found in Appendix 3.3.

Species traits

For both butterflies and plants relevant traits contributing to the adaptive capacity of the ecosystem were selected *a priori* to capture species resistance to, and recovery after disturbance (Tables 3.2, 3.3). Butterflies are assumed to be more resistant to disturbances when they hibernate as pupae or adults, tolerate a large variation in moisture conditions, or have large habitat area requirement. Butterflies are assumed to be less resistant to disturbance when they hibernate as eggs or larvae, tolerate a narrow moisture range, or have small habitat area requirement. The rationale behind this lower species vulnerability with wide moisture ranges and large area requirements is readily found in the lower effects of environmental variability on species. Species hibernating as eggs or larvae are more susceptibility to unsuitable spring conditions and generally have slower growth rates, and are thus more vulnerable (Bink 1992; WallisDeVries and Van Swaay 2006). Trait, such as a high number of eggs, high vagrancy and high voltinism, are associated with an increase in recovery (Burke et al. 2011; Borschig et al. 2013). For vascular plants, traits associated with high resistance are low Specific Leaf Area (SLA), occurrence of below ground perennial buds, large canopy height, small leaves and presence of aerenchyma (Cornelissen et al. 2003; Kleyer et al. 200; van Groenendael et al. 1996). Clonal growth, long distance dispersal, large lateral spread, long seed longevity and high seed mass are important for recovery (Ehrlen and Eriksson 2000; Schleicher et al. 2011; McConkey et al. 2012). Trait values for each species were obtained from the literature and/or from expert judgement (Tables 3.2, 3.3).

Table 3.2. Butterfly traits with their classes included in the analyses. The top three traits are related to resistance. The bottom three are related to recovery.

	Trait	Type of variable	Classes	Literature
Resistance				
1	Hibernate stage	Ordinal	1 = egg 2 = larva 3 =pupa 4 = butterfly	Bink (1992)
2	Moisture range	Continuous	Index 1 - 12	Oostermeijer and Van Swaay (1998)
3	Habitat area requirement	Continuous	Quantitative (ha)[a]	Bink (1992)
Recovery				
4	Number of eggs	Continuous	Quantitative[a]	Bink (1992)
5	Vagrancy	Ordinal	Index 1 – 9	Bink (1992)
6	Voltinism	Ordinal	1 = 1 brood per year 2 = more than 1 broods per year (maximum 4)	Bink (1992)

[a] trait log-10 transformed for analyses

Table 3.3. Traits used for plants with their classes included in the analyses. The top five traits are related to resistance. The bottom seven traits are related to recovery.

	Ttrait	Type of variable	Classes	Literature
Resistance				
1	Specific Leaf Area	Continuous	Quantitative (mm^2)[a]	Kleyer et al. (2008)
2	Growth form	Nominal	Perennial buds: 1= above ground 2= below ground	Kleyer et al. (2008)
3	Canopy height	Continuous	Quantitative (m)[a]	Poschlod et al. (2003), Fitter and Peat (1994)
4	Leaf size	Continuous	Quantitative (mm^2)[a]	Poschlod et al. (2003); Klotz et al. (2002); Kleyer et al. (2008) ; expert knowledge
5	Aerenchyma	Nominal	1=yes 2=no	Kleyer et al. (2008); Klotz et al. (2002)
Recovery				
6	Clonal growth	Nominal	1=yes 2=no	Klimešová and Klimeš; Klimešová and de Bello
7	Dispersal mode other	Ordinal	1=yes 2=no[b]	Bouman et al. (2000); Royal Botanic Gardens Kew (2008); Kleyer et al. (2008)
8	Dispersal mode water	Ordinal	1=yes 2=no	Bouman et al. (2000); Royal Botanic Gardens Kew (2008); Kleyer et al. (2008)
9	Dispersal mode wind	Ordinal	1=yes 2=no	Bouman et al. (2000); Royal Botanic Gardens Kew (2008)’ Kleyer et al. (2008)
10	Lateral spread	Ordinal	1= 0 (m) 2= <0.01 (m) 3= <0.25 (m) 4= >0.25 (m)	Klimešová and Klimeš; Klimešová and de Bello; Kleyer et al. (2008)
11	Seed longevity	Ordinal	1=transient 2=short term 3=long term	Klotz et al. (2002)
12	Seed mass	Continuous	Quantitative (g)	Royal Botanic Gardens Kew (2008)

[a]trait log-10 transformed for analyses; [b]includes bird feed, ants, spilling, mammalian dung, mammalian fur, bird droppings.

Relating heterogeneity to traits

To detect relationships between heterogeneity metrics and traits via species abundance, we conducted a three-table joint analysis named RLQ analysis (Doledec et al. 1996; Dray and Legendre 2008). This approach allows the joint analysis of 3 data matrices: heterogeneity metrics x study areas (table R), study areas x species (table L) and traits x species (table Q). Because we were interested in the effect of heterogeneity at different spatial extents, the analysis was conducted per radius. In this example, we use Hill-Smith analysis to summarize the traits tables containing a mix of quantitative and qualitative values (Dray and Legendre 2008). To relate spatial heterogeneity to butterfly traits we created three tables **R**, **L** and **Q**, with the values of six heterogeneity metrics (Table 3.1) in sixteen study areas, the abundance of nineteen butterfly species in sixteen study areas, and the values of six traits (Table 3.2) of the nineteen butterfly species, respectively. For plants we created **R**, **L** and **Q** tables with the values of six heterogeneity metrics (Table 1) in thirteen study areas, the presence of 120 plant species in thirteen study areas, and the values of ten traits (Table 3.3) of the 120 plant species, respectively. RLQ is an extension of co-inertia analysis that simultaneously finds linear combinations of the variables of table R and linear combinations of the variables of table Q of maximal covariance weighted by the data in table L. To relate the heterogeneity metrics and the functional traits the individual analyses are combined to maximize the co-variation between heterogeneity metrics and functional traits (Duchamp and Swihart 2008).

With a fourth-corner analysis (Model 6; Legendre et al. 1997; Dray and Legendre 2008; Dray et al. 2014) we tested the statistical significance of the relationship between functional trait categories and variability in the heterogeneity indices through the link provided by the abundance data. The fourth-corner analysis considers all correlations between traits. We used 49 999 permutations to estimate P-values. As multiple correlations are being tested, the false discovery rate (FDR) adjustment for multiple testing (Benjamini and Hochberg 1995; Dray et al. 2014) was applied on the P-values. Only the correlations that remained significant after correction were used for the interpretation. All calculations were made with the ade4 -package (Dray and Dufour 2007).

3.3 Results

RLQ analysis butterflies

The RLQ analysis revealed a significant association between heterogeneity metrics and traits for the 1, 2 and 5 km radius ($P = 0.007$, 0.003 and 0.004 respectively, based on a permutation test for the total co-inertia). The correspondence analysis determined L table canonical correlations of 0.29, 0.29 and 0.27 (Table 3.4), indicating that the L table has weak potential to link heterogeneity metrics (R) to traits (Q). In the RLQ analysis, 82%, 89% and 91% of the heterogeneity variance, as captured by the PCA, was explained by the first two RLQ axes. For the traits 95%, 87% and 82% of the variance captured by the PCA was explained by the first two RLQ axes. These results indicate that the RLQ analysis linked substantial portions of variation of heterogeneity to traits through the butterfly abundances for the 1, 2 and 5 km radius.

For the 1 km radius, the first axis of the RLQ analysis showed the strongest positive relation with the length of ditches and the Shannon-Wiener *H'* Index and the strongest negative relation with the contagion *H'* index and the contagion *L'* index (Figure 3.3A). Therefore, the main environmental gradient related strongest to the butterfly traits, stretches from a heterogeneous wetland with fine-scale variation in wet to dry conditions, to a homogeneous landscape with high configuration and a low diversity of habitat types. The heterogeneous landscape is positively related to the occurrence of the traits high vagrancy, high voltinism and a large habitat area requirement. The homogeneous landscape is negatively related to those traits. The positive part of the first axis of the 2 km radius highlights a homogenous landscape with high contagion *H'* index and long total length of hedgerows, and the negative part highlights long total length of ditches (Figure 3.3B). Landscapes with high habitat configuration, long total length of hedgerows and low total length of ditches are positively related to low vagrancy, low voltinism and a small habitat area requirement. The first axis of the 2 km radius is related to the same butterfly species as the first axis of the 1 km radius. The results for the 5 km radius are similar to the results of the 2 km radius (Figure 3.3C).

Table 3.4. Results of the RLQ analysis of butterfly traits for the 1, 2 and 5 km radius.

RLQ axes	1 km		2 km		5 km	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Eigenvalues	0.317	0.089	0.444	0.069	0.338	0.126
Covariance	0.562	0.299	0.667	0.263	0.582	0.354
Correlation	0.285	0.192	0.289	0.182	0.271	0.232
R/RLQ	75%	82%	91%	89%	66%	91%
L/RLQ	51%	40%	52%	38%	48%	48%
Q/RLQ	88%	95%	91%	87%	89%	82%

R/RLQ represents the percentage of the variance of the separate analysis of table R (heterogeneity metrics x study areas) accounted for by each of the first two ordination axes of the RLQ analyses. L/RLQ is the same for the separate analysis of table L (study areas x butterfly species) and Q/RLQ is the same for the separate analysis of table Q (traits x butterfly species). It is calculated as the ratio of the axis eigenvalue of RLQ analysis on the corresponding axis eigenvalue of separate analysis.

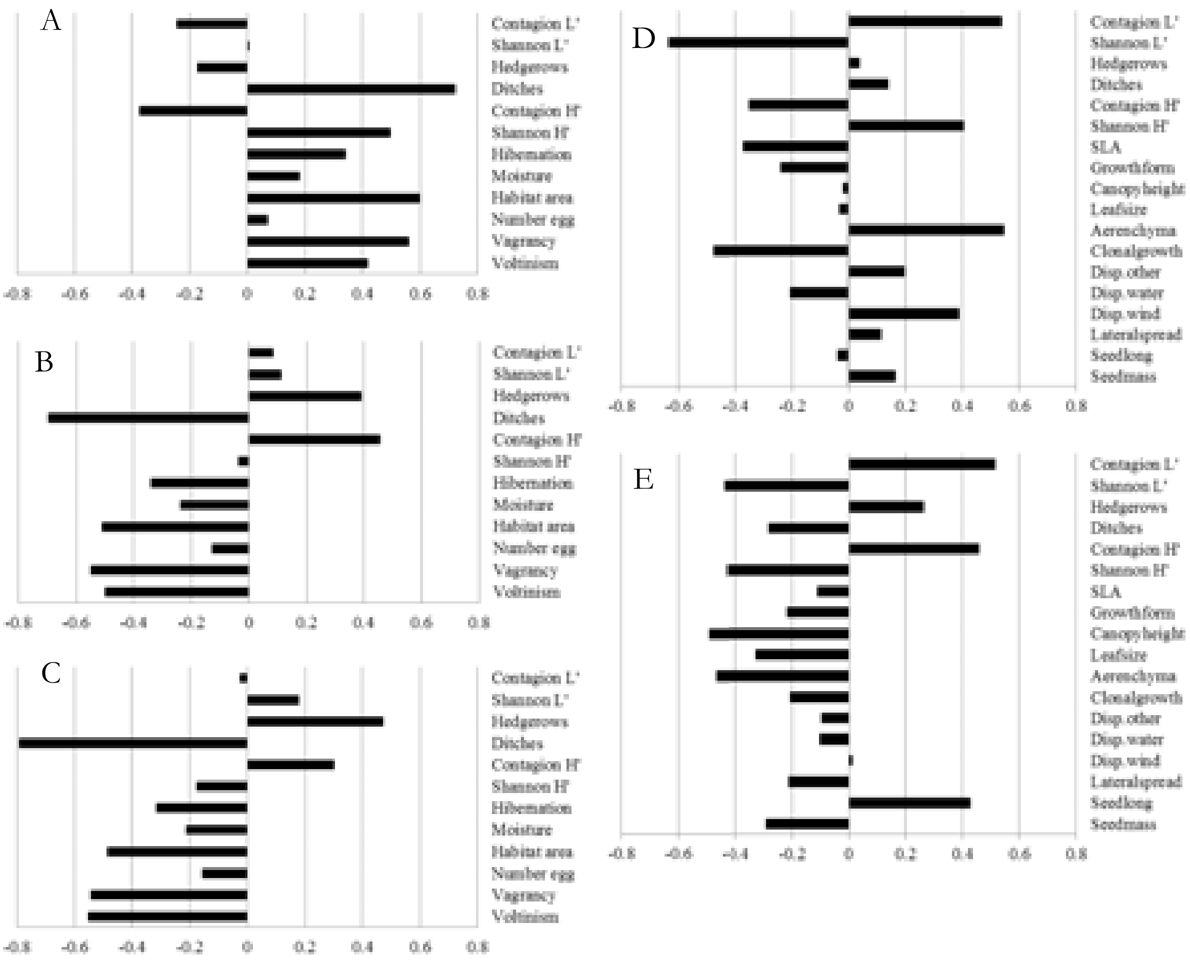

Figure 3.3. Graphical display of RLQ scores along RLQ axis 1 of traits and heterogeneity metrics. For the butterflies: (A) 1 km radius, (B) 2 km radius, (C) 5 km radius. The top six are heterogeneity metrics. See Table 1 for the codes of the metrics. The bottom six are butterfly traits. See Table 2 for the codes of the traits. For the plants: (D) 1 km radius, (E) 5 km radius. The top six are heterogeneity metrics. See Table 1 for the codes of the metrics. The bottom 12 are plant traits. See Table 3.3 for the codes of the traits.

Table 3.5. Results from fourth-corner analysis using 19 butterfly species. Numbers indicate P-values of relationships between pairs of traits and heterogeneity metrics for the 1, 2 and 5 km radius (symbols as in Tables 3.1, 3.2).

	Contagion L’			Shannon L’			Hedgerows			Ditches			Contagion H’			Shannon H’		
Radius	1	2	5	1	2	5	1	2	5	1	2	5	1	2	5	1	2	5
Hibernation	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**0.047 +**	**0.041 +**	**0.050 +**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Moisture	n.s.	n.s.	**0.045 -**	n.s.	n.s.	n.s.	n.s.	**0.037 -**	**0.019 -**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Habitat	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**0.011 +**	**0.009 +**	**0.015 +**	**0.011 -**	**0.011 -**	n.s.	**0.003 +**	**0.036 +**	n.s.
Number egg	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**0.010 -**	**0.033 -**	**0.037 -**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Vagrancy	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**0.010 +**	**0.006 +**	**0.013 +**	n.s.	**0.020 -**	n.s.	**0.02 +**	**0.015 +**	n.s.
Voltinism	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**0.034 -**	n.s.	**0.018 +**	**0.012 +**	**0.012 +**	n.s.	n.s.	**0.036 -**	n.s.	**0.021 +**	n.s.

Plus and minus signs indicate the direction of significant relationships; n.s., non-significant relationship (>0.05).

RLQ analysis plants

The RLQ analysis revealed significant associations between heterogeneity metrics and traits for the 1 and 5 km radius (P = 0.006 and 0.009 respectively, based on a permutation test for the total co-inertia). We did not found significant associations for the 2 km radius and therefore we will not show or discuss these results. From the correspondence analysis of the L table canonical correlations of 0.14, 0.11 and 0.15 were found (Table 3.6), indicating that the L table has weak potential to link heterogeneity metrics (R) to traits (Q). In the RLQ analysis, 77%, 80% and 97% of the heterogeneity variance, as captured by the PCA, was explained by the first two RLQ axes. For the traits 77%, 56% and 70% of the variance captured by the PCA, was explained by the first two RLQ axes. These results indicate that the RLQ analysis was able to link substantial portions of variation of heterogeneity metrics to traits through the plant presence for the 1 and 5 km radius. For the 1 km radius the first RLQ axis identifies associations between the contagion *L'* index, Shannon-Wiener *H'* Index, aerenchyma and dispersal mode wind (Figure 3.3D). And a landscape with a high Shannon-Wiener *L'* Index characterized by species with clonal growth and high SLA. The 5 km radius showed the strongest positive relation with the contagion *L'* index and the contagion *H'* index and the strongest negative relation with the Shannon-Wiener *H'* Index and the Shannon-Wiener *L'* Index (Figure 3.3E). Therefore, the main environmental gradient related to the plant traits, stretches from a homogeneous to a heterogeneous landscape. The homogeneous landscape is associated with species with high canopy height and aerenchyma. The heterogeneous landscape identifies species with long seed longevity.

Table 3.6 Results of the RLQ analysis of plants traits for the 1, 2 and 5 km radius

RLQ axes	1 km		2 km		5 km	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Eigenvalues	0.020	0.012	0.012	0.008	0.023	0.013
Covariance	0.136	0.111	0.112	0.090	0.152	0.111
Correlation	0.094	0.058	0.079	0.058	0.065	0.086
R/RLQ	74%	77%	73%	80%	97%	97%
L/RLQ	27%	23%	23%	22%	19%	33%
Q/RLQ	45%	77%	41%	56%	70%	70%

R/RLQ represents the percentage of the variance of the separate analysis of table R (heterogeneity metrics x study areas) accounted for by each of the first two ordination axes of the RLQ analyses. L/RLQ is the same for the separate analysis of table L (study areas x plant species) and Q/RLQ is the same for the separate analysis of table Q (traits x plant species). It is calculated as the ratio of the axis eigenvalue of RLQ analysis on the corresponding axis eigenvalue of separate analysis.

Fourth-corner analysis plants

Plant traits are not significantly associated with the heterogeneity metrics in the fourth-corner analysis. Therefore, single traits were not considered to be affected by heterogeneity metrics.

3.4 Discussion

In this study we demonstrate that spatial heterogeneity has effects on the abundance of traits related to resistance and recovery for butterflies and vascular plants. In addition, we found that the spatial extent at which heterogeneity has the strongest impact on traits differed between the two species groups. However, our results did not support the hypothesis that larger spatial extent would be more relevant for butterflies and the smaller spatial extent for plants. Moreover, there were no significant relationships between single plant traits and heterogeneity metrics.

Some of the results presented in this research are supported by earlier studies. Besides environmental factors, spatial structures at local extent affected variation in community-level traits of stream fish (Michel and Knouft 2014). Correlation in species richness between taxa increased with increasing spatial heterogeneity, tested for butterflies, plants and farmland birds in relation to habitat type, heterogeneity, land-use intensity and spatial scale (Ekroos et al. 2013). These results likely support the hypothesis of Tscharntke et al. (2012) assuming that environmental changes do not affect species traits equally. We used RLQ and fourth corner analyses to quantify which traits caused the greatest species response to spatial heterogeneity and spatial extent, showing that the heterogeneity metrics and spatial extent relate to traits concerning resistance and recovery of butterflies and plants. However, spatial heterogeneity had different effects on the butterfly and plant traits, showing that distinct mechanisms drive the response of these species.

Relationship between spatial heterogeneity and butterfly traits

We examined whether changes in traits occur as a consequence of spatial heterogeneity at different spatial extents. For all three radiuses, the RLQ analysis for butterflies indicates a positive relationship between spatial heterogeneity and species with high vagrancy, more than one brood per year and a large habitat requirement. Butterflies with high vagrancy are better dispersers than butterflies with low vagrancy. Therefore butterflies with high vagrancy can colonise new habitat after disturbance. Butterflies with low voltinism tend to overwinter as eggs or larvae. As argued by WallisDeVries and Van Swaay (2006), this implies a greater dependence of these species on warm microclimatic conditions in spring than for species that tend to overwinter as pupae or adults (high voltinism). Butterflies with large habitat requirement have more chance to find suitable habitat in a variabele environment. So, high vagrancy, more than one brood per year and a large habitat requirement indicate strong resistance and recovery to environmental disturbance and, consequently, a positive effect on the adaptive capacity of the ecosystem (WallisDeVries, 2014). The fourth-corner analysis shows the same trend as the RLQ analysis with the most significant correlations for the 2 km radius. Vagrancy, voltinism, habitat area requirement and hibernation stage are positive correlated with the Shannon-Wiener *H'* Index and total length of ditches. This high number of significant relations is linked to the heterogeneity gradient (also depicted by RLQ axis 1) and indicates strong species' resistance and recovery to environmental disturbance enhancing the adaptive capacity of the ecosystem. The Shannon L' index did not correlate with any selected traits for butterflies as landscape types are apparently uncorrelated with critical resources (categories do not reflect habitat features as well as in Shannon H' index). Other significant results (e.g., the negative correlations between number of eggs and hedgerows, and between moisture range and hedgerows) suggest a weak resistance and weak recovery of species to environmental disturbance and, hence, does not contribute to the adaptive capacity of the ecosystem. (WallisDeVries 2014). The examined linear landscape elements (i.e. ditches and hedgerows) reflect abiotic conditions and land use. In the drier parts of the Netherlands we find enclosed landscapes where hedgerows traditionally fenced fields on sandy soils. Also, crop were cultivated on sandy soils and some (e.g., maize) were accompanied with high fertilizer loads. Ditches are characteristic for the Dutch extensive peat-lands in the wetter parts where land-use has been intensified and grasslands are currently the main vegetation type. Our results indicate that landscapes with high heterogeneity and a long total ditch length are likely to select for butterflies with traits related to high resistance and recovery. Sedentary butterfly species are expected to respond on a finer spatial scale to heterogeneity compared to more mobile species. Also one would expect that habitat generalists would benefit from a higher variability of heterogeneity compared to habitat specialists (e.g., Devictor et al. 2010; Ockinger et al. 2012; Borschig et al. 2013). However, in the RLQ analysis the difference between radiuses was not pronounced. This result, and its discrepancy with our expectations, can be explained by the occurrence of selected specialists, such as *H. morpheus* and *P. alcon*. The rareness of these butterfly species is not only influenced by spatial heterogeneity but also by local management and other abiotic conditions (Menendez et al. 2007; WallisDeVries 2004). Borschig et al. (2013) studied if ecological and life-history traits differ between butterfly communities with different land-use intensities. Their results show homogenisation of the butterfly communities from specialists to generalists with increasing land-use intensity. The same was found for habitat modification and climate change (Warren et al. 2001; Thomas et al. 2001). The fourth-corner method suggests a gradient from wet to dry in the studied areas with specialists occurring rather in the sandy areas where they find a greater variation in micro-climates and the generalists being more abundant in the peat-lands where greater mobility and reproductive capacity proves advantageous.

Our results suggest that the heterogeneity metrics relate strongest to traits concerning resistance and recovery of butterflies, rather than the spatial scale. This may be due to correlation between heterogeneity metrics, but as all descriptors of heterogeneity were included, their relative effect on trait composition could be identified (Smith et al. 2009). Another possible explanation for the discrepancy of our findings from Tscharntke et al.'s (2012) hypothesis is that, due to the varied size of the studied wetlands, a clear environmental gradient in the spatial extents is missing. To determine the scale of effect we selected 3 increasing spatial extents. We expect the 1 km radius to be mostly suitable habitat types, 2 km radius to be a transition between suitable habitat and other landscape types and at the 5 km radius variability among types to be minimal. However, the selected study areas were limited by the available data of butterflies and plants. Resulting in a reduction of the gradient across spatial extents which reduces the chance of detecting associations between heterogeneity metrics and traits.

Relationship between landscape heterogeneity and plant traits

The RLQ analysis of the 1 km radius for plants indicates a positive relationship between a heteregenous wetland and the proportion of typical pioneer species with aerenchyma and a high ability of seed dispersal by wind and low SLA. On the other hand, spatial heterogeneity positively relates to the proportion of longlived species with clonal growth and a high SLA. In general, pioneer species can be classified as ruderals that invest much resources in reproductive output (e.g., Grime 1977) and therewith in the ability for fast recovery at larger spatial extent. Longlived species with clonal growth include both species with a high ability to tolerate stressfull conditions and species with a high competitive ability. In comparision to the former group these species have in general a higher local resistance and stronger ability for local recovery with environmental disturbances (i.e. through vegetative expansion over short distance and therefore contribute more to the adaptive capacity of the ecosystem (Lindborg et al. 2012)). The results show that the combination of landscape types and configuration can serve as source for (re)colonisation of areas (Tscharntke et al. 2012). The results for the 5 km radius show a different pattern. Homogeneous wetlands with long total length of hedgerows are positively related to the proportion of species with a persistent soil seed bank. The ability of species to accumulate a long-term persistent seed bank (i.e. a high seed longevity) can buffer species against local extinction (e.g., Ozinga et al. 2009) and contribute to the ability for a fast recovery after local disturbances. Heterogeneous wetlands with long total length of ditches are characterized by a high proportion of plant species with high canopy height, aerenchyma, large leafsize and high seedmass. This can contribute to a strong resistance and strong recovery to environmental disturbances, resulting in potentially high adaptive capacity of the ecosystem. Though the relationship between heterogeneity and traits is less pronounced for plants than for butterflies. This is probably related to the immobility of the major part of the life-cycle of vascular plants (with the exception of seed dispersal) and their delayed response to changes in local abiotic conditions (Lindborg 2007; Gazol and Ibáñez, 2010). As a consequence the relationship between traits and the landscape will probably be weaker and more indirect (Lebrija-Trejos et al. 2010). As an example, landscape composition and configuration had different effects on carabid and plant dispersal traits, showing that distinct mechanisms drive the response of the two taxa (Duflot et al. 2014). Perhaps this can be assigned to the strong influence of spatio-temporal scales (Tscharntke 2012; Drenovsky et al. 2012) wherein species function (also read Peterson et al. 1998). Several studies demonstrated that in agricultural landscapes short-term and long-term changes represent important drivers of species diversity (Burel et al. 1998; Kleijn et al. 2001;

Ernoult and Alard, 2011). Implying that inappropriate selection of time and spatial extent at which drivers are identified can yield misleading results. Hence, other environmental factors can have distorted the relationships investigated, and further research is worth to be achieved.

Importance of landscape heterogeneity linked to resilience

The potential links between trait composition and ecosystem functioning requires further research and discussion. Depending on the two processes (resistance and recovery) that contribute to the adaptive capacity of the ecosystem we are able to better understand how changes in community composition could modify ecosystem functioning. Our results for butterflies and plants reflect a difference in functional divergence-convergence in response to spatial heterogeneity at different spatial extents. Although it is accepted that effects of environmental variables lead in general to trait-convergence, whereas effects of biotic interactions and disturbance often lead to trait-divergence (Ackerly 2003; Grime 2006; McGill et al. 2006), no study to date has shown the relation between spatial heterogeneity at different spatial extents and traits of butterflies and plants. Moretti and Legg (2009) related the distributions of traits of plants and animals in forests affected by regular winter fires. They found a strong association between plant and animal traits under fire constraints and suggest that disturbance by fire prompts a convergent selection of traits associated with persistence and resilience. However, their study ignored different spatial extents whereby they miss the effects of environmental change on the spatial determinants of traits (Michel and Knouft 2014). Oliver et al. (2010) did considered 1, 2 and 5 km radiuses around the centre of their study sites. Their findings show that the larger landscapes had the strongest effects on the more mobile butterfly species. These findings possibly support the habitat heterogeneity hypothesis (MacArthur and Wilson 1967) at the species level, demonstrating the coexistence of species with different traits in a more heterogeneous landscape, probably due to niche differentiation and functional trade-offs (Viard-Cretat et al. 2011).

3.5 Conclusion

Our results contribute to the understanding of interactions between landscape properties and ecosystem functioning through the response of species traits. We showed that a higher spatial heterogeneity will select for a species composition with a higher adaptive capacity to disturbances (e.g., climate change). The results of our study suggest that considering environmental variables at multiple spatial extents may provide better information about the ecological needs of a species, than at a single extent. Thus, managers and policy makers should take into account the configuration of the landscape at different spatial extents surrounding wetlands in order to promote the conditions for ecological resilience, by stimulating wetland related heterogeneity such as ditches, water, reed land, wet forests and natural grasslands.

Appendix 3.1

Table A.3.1 Butterfly species included in the study.

	Species
1	Anthocharis cardamines
2	Apatura iris
3	Aphantopus hyperantus
4	Boloria selene
5	Callophrys rubi
6	Carterocephalus palaemon
7	Heteropterus morpheus
8	Lasiommata megera
9	Limenitis camilla
10	Lycaena tityrus
11	Phengaris alcon
12	Favonius quercus
13	Ochlodes sylvanus
14	Pararge aegeria
15	Pieris brassicae
16	Plebejus argus
17	Pyrgus malvae
18	Pyronia tithonus
19	Thymelicus sylvestris

Appendix 3.2

Table A.3.2 Plant species included in the study.

	Species
1	Achillea ptarmica
2	Acorus calamus
3	Agrostis canina
4	Agrostis capillaris
5	Agrostis stolonifera
6	Ajuga reptans
7	Alopecurus geniculatus
8	Anthoxanthum odoratum
9	Atriplex prostrata
10	Bellis perennis
11	Bromus hordeaceus
12	Caltha palustris s. palustris
13	Capsella bursa-pastoris
14	Cardamine flexuosa
15	Cardamine pratensis
16	Carex acutiformis
17	Carex disticha
18	Carex echinata
19	Carex elata
20	Carex elongata
21	Carex nigra
22	Carex panicea
23	Carex riparia
24	Carex rostrata
25	Cerastium fontanum s. vulgare
26	Ceratocapnos claviculata
27	Cicuta virosa
28	Cirsium arvense
29	Cirsium dissectum
30	Cirsium vulgare
31	Dactylis glomerata
32	Danthonia decumbens
33	Drosera rotundifolia
34	Eleocharis palustris
35	Elytrigia repens
36	Epilobium palustre
37	Epilobium parviflorum
38	Epilobium tetragonum
39	Equisetum arvense

40	Equisetum fluviatile
41	Erica tetralix
42	Eriophorum angustifolium
43	Festuca pratensis
44	Festuca rubra
45	Filipendula ulmaria
46	Galeopsis bifida
47	Galeopsis tetrahit
48	Galium aparine
49	Galium palustre
50	Galium uliginosum
51	Glechoma hederacea
52	Glyceria fluitans
53	Hierochloe odorata
54	Holcus lanatus
55	Holcus mollis
56	Hydrocotyle vulgaris
57	Hypericum tetrapterum
58	Hypochaeris radicata
59	Iris pseudacorus
60	Juncus articulatus
61	Juncus bufonius
62	Juncus conglomeratus
63	Juncus effusus
64	Juncus subnodulosus
65	Lathyrus palustris
66	Leontodon autumnalis
67	Lolium perenne
68	Lotus pedunculatus
69	Luzula campestris
70	Luzula multiflora
71	Lychnis flos-cuculi
72	Lycopus europaeus
73	Lysimachia nummularia
74	Lysimachia thyrsiflora
75	Lythrum salicaria
76	Matricaria discoidea
77	Mentha aquatica
78	Menyanthes trifoliata
79	Molinia caerulea
80	Myosotis laxa s. cespitosa
81	Oxycoccus palustris
82	Plantago lanceolata
83	Plantago major

84	Poa annua
85	Poa pratensis
86	Poa trivialis
87	Polygonum aviculare
88	Potentilla anglica
89	Potentilla anserina
90	Potentilla erecta
91	Potentilla palustris
92	Prunella vulgaris
93	Ranunculus acris
94	Ranunculus ficaria s. bulbilifer
95	Ranunculus flammula
96	Ranunculus lingua
97	Ranunculus repens
98	Ranunculus sceleratus
99	Rorippa amphibia
100	Rorippa palustris
101	Rumex acetosa
102	Sagina procumbens
103	Sagittaria sagittifolia
104	Salix repens
105	Scutellaria galericulata
106	Senecio aquaticus
107	Sium latifolium
108	Sparganium erectum
109	Stachys palustris
110	Stellaria media
111	Stellaria palustris
112	Symphytum officinale
113	Taraxacum officinale
114	Thalictrum flavum
115	Trifolium pratense
116	Trifolium repens
117	Triglochin palustris
118	Valeriana dioica
119	Valeriana officinalis
120	Viola palustris

Appendix 3.3

Table A.3.3 Heterogeneity indices used in the analysis. Area codes refer to the maps in Figure 3.1. Codes of the heterogeneity indices can be found in Table 3.1.

Study area	Area code	Butterfly /Plant	Radius in km	ContagionL	ShannonL	Hedgerows	Ditches	ContagionH	ShannonH
Ackerdijkse Plassen	ap	Plant	1	0.582	1.388	1584	52123	0.604	0.728
Ackerdijkse Plassen	ap	Plant	2	0.684	1.053	9380	219884	0.606	0.743
Ackerdijkse Plassen	ap	Plant	5	0.656	1.287	104498	803947	0.666	0.819
Ackerdijkse Plassen	ap	Butterfly	1	0.553	1.352	1777	52243	0.623	0.687
Ackerdijkse Plassen	ap	Butterfly	2	0.69	1.09	12550	211814	0.588	0.779
Ackerdijkse Plassen	ap	Butterfly	5	0.66	1.274	105047	807853	0.665	0.824
Broekland	bl	Butterfly	1	0.646	1.299	2364	33900	0.903	0.111
Broekland	bl	Butterfly	2	0.588	1.505	18023	70815	0.805	0.22
Broekland	bl	Butterfly	5	0.594	1.668	166119	225808	0.849	0.363
Bennekomse Meent	bm	Butterfly	1	0.642	1.243	10534	29654	0.573	0.838
Bennekomse Meent	bm	Butterfly	2	0.613	1.343	46871	78630	0.601	0.788
Bennekomse Meent	bm	Butterfly	5	0.619	1.568	254457	233039	0.675	0.847
Moerputten	bw	Butterfly	1	0.535	1.505	6094	25362	0.707	0.384
Moerputten	bw	Butterfly	2	0.539	1.602	29531	72953	0.638	0.461
Moerputten	bw	Butterfly	5	0.571	1.771	170020	309035	0.661	0.866
Nieuwkoop	dm	Butterfly	1	0.666	1.116	1598	72733	0.631	0.885
Nieuwkoop	dm	Butterfly	2	0.619	1.348	3016	228653	0.51	1.136
Nieuwkoop	dm	Butterfly	5	0.66	1.205	46938	1157843	0.568	1.004
Gagelpolder	gp	Butterfly	1	0.493	1.741	6674	64894	0.512	1.052
Gagelpolder	gp	Butterfly	2	0.543	1.617	19956	203747	0.566	0.963
Gagelpolder	gp	Butterfly	5	0.617	1.523	138919	913187	0.59	0.929
Korenburgerveen	kbv	Plant	1	0.575	1.71	6758	15637	0.825	0.444
Korenburgerveen	kbv	Plant	2	0.581	1.703	34157	39382	0.721	0.731
Korenburgerveen	kbv	Plant	5	0.627	1.51	234449	187519	0.582	1.103
Korenburgerveen	kbv	Butterfly	1	0.565	1.765	5194	13264	0.755	0.625
Korenburgerveen	kbv	Butterfly	2	0.582	1.688	31732	37885	0.727	0.712
Korenburgerveen	kbv	Butterfly	5	0.63	1.504	218530	189335	0.583	1.096

Laagbroek	lb	Butterfly	1	0.599	1.549	7503	10621	0.833	0.377
Laagbroek	lb	Butterfly	2	0.604	1.53	29612	41469	0.797	0.457
Laagbroek	lb	Butterfly	5	0.631	1.501	166117	167221	0.663	0.838
Luttenbergerven	lbv	Plant	1	0.561	1.492	11182	8252	0.589	0.57
Luttenbergerven	lbv	Plant	2	0.637	1.328	36135	30739	0.516	0.671
Luttenbergerven	lbv	Plant	5	0.685	1.291	233697	167357	0.702	0.795
Luttenbergerven	lbv	Butterfly	1	0.562	1.496	12138	6798	0.538	0.641
Luttenbergerven	lbv	Butterfly	2	0.634	1.34	37549	26720	0.545	0.631
Luttenbergerven	lbv	Butterfly	5	0.69	1.271	235921	169746	0.7	0.8
Loosdrecht	ld	Butterfly	1	0.461	1.808	4878	38755	0.42	1.343
Loosdrecht	ld	Butterfly	2	0.47	1.829	11893	139181	0.458	1.252
Loosdrecht	ld	Butterfly	5	0.561	1.776	95043	633440	0.63	0.904
Leusveld	leuv	Butterfly	1	0.626	1.267	11259	10288	0.68	0.423
Leusveld	leuv	Butterfly	2	0.664	1.346	49340	35562	0.662	0.891
Leusveld	leuv	Butterfly	5	0.631	1.516	208071	198815	0.719	0.731
Lindevallei	lv	Plant	1	0.493	1.666	4002	38536	0.465	1.008
Lindevallei	lv	Plant	2	0.531	1.702	10260	130860	0.436	1.332
Lindevallei	lv	Plant	5	0.645	1.426	121282	648169	0.463	1.273
Lindevallei	lv	Butterfly	1	0.499	1.65	3988	38324	0.479	0.98
Lindevallei	lv	Butterfly	2	0.538	1.675	10029	131246	0.444	1.321
Lindevallei	lv	Butterfly	5	0.645	1.428	120415	647946	0.463	1.274
Moerputten	moep	Plant	1	0.586	1.347	7017	26289	0.749	0.332
Moerputten	moep	Plant	2	0.577	1.571	29799	71930	0.66	0.425
Moerputten	moep	Plant	5	0.569	1.782	168829	307934	0.661	0.866
Molenpolder-Westbroek	mop	Plant	1	0.597	1.433	3013	81282	0.449	1.229
Molenpolder-Westbroek	mop	Plant	2	0.558	1.554	15863	254429	0.536	1.015
Molenpolder-Westbroek	mop	Plant	5	0.604	1.576	140640	1011331	0.581	0.964
Nieuwkoop	nk	Plant	1	0.736	0.898	1208	73385	0.784	0.431
Nieuwkoop	nk	Plant	2	0.684	1.101	6088	243357	0.53	1.082
Nieuwkoop	nk	Plant	5	0.678	1.138	40323	1188416	0.572	0.994
Ottema Wiersma	ow	Plant	1	0.593	1.478	5632	42994	0.547	1.062
Ottema Wiersma	ow	Plant	2	0.679	1.184	27756	151150	0.545	1.083
Ottema Wiersma	ow	Plant	5	0.689	1.273	288842	850802	0.551	1.089
Rheezermaten	rm	Butterfly	1	0.577	1.686	4296	6826	0.684	0.751
Rheezermaten	rm	Butterfly	2	0.578	1.709	19491	24962	0.647	0.879
Rheezermaten	rm	Butterfly	5	0.604	1.626	152024	174516	0.63	0.945
Tondense Heide	th	Butterfly	1	0.69	1.127	5415	10111	0.521	0.665
Tondense Heide	th	Butterfly	2	0.745	1.023	33143	42135	0.638	0.952
Tondense Heide	th	Butterfly	5	0.67	1.338	195357	223415	0.628	0.963
Veerslootlanden	vsl	Plant	1	0.836	0.608	3766	58627	0.594	1.042
Veerslootlanden	vsl	Plant	2	0.812	0.7	26122	217635	0.641	0.861
Veerslootlanden	vsl	Plant	5	0.697	1.111	252922	1027373	0.61	0.927

Veerslootlanden	vsl	Butterfly	1	0.777	0.828	6365	62856	0.682	0.777
Veerslootlanden	vsl	Butterfly	2	0.763	0.866	31107	201045	0.65	0.789
Veerslootlanden	vsl	Butterfly	5	0.701	1.097	239833	1050770	0.601	0.954
Wieden	w	Plant	1	0.535	1.506	1094	39229	0.555	1.061
Wieden	w	Plant	2	0.545	1.668	2627	126296	0.55	1.102
Wieden	w	Plant	5	0.541	1.722	66655	829044	0.59	1.022
Weerterbos	wb	Butterfly	1	0.663	1.256	4351	13545	0.556	0.942
Weerterbos	wb	Butterfly	2	0.624	1.579	22578	40979	0.752	0.654
Weerterbos	wb	Butterfly	5	0.6	1.672	142187	193500	0.657	0.883
Weerribben_1	wr	Plant	1	0.551	1.082	76	22043	0.521	1.001
Weerribben_1	wr	Plant	2	0.584	1.471	3432	121538	0.509	1.078
Weerribben_1	wr	Plant	5	0.542	1.689	44611	788901	0.44	1.256
Weerribben_2	wr	Plant	1	0.678	1.048	279	32431	0.691	0.619
Weerribben_2	wr	Plant	2	0.595	1.468	1674	124235	0.557	0.959
Weerribben_2	wr	Plant	5	0.521	1.775	35431	754439	0.454	1.24
Zuidlaardermeer	zlm	Plant	1	0.63	1.259	166	58303	0.64	0.736
Zuidlaardermeer	zlm	Plant	2	0.585	1.562	11610	151343	0.502	1.046
Zuidlaardermeer	zlm	Plant	5	0.563	1.825	129153	595805	0.604	1.022

Appendix 3.4

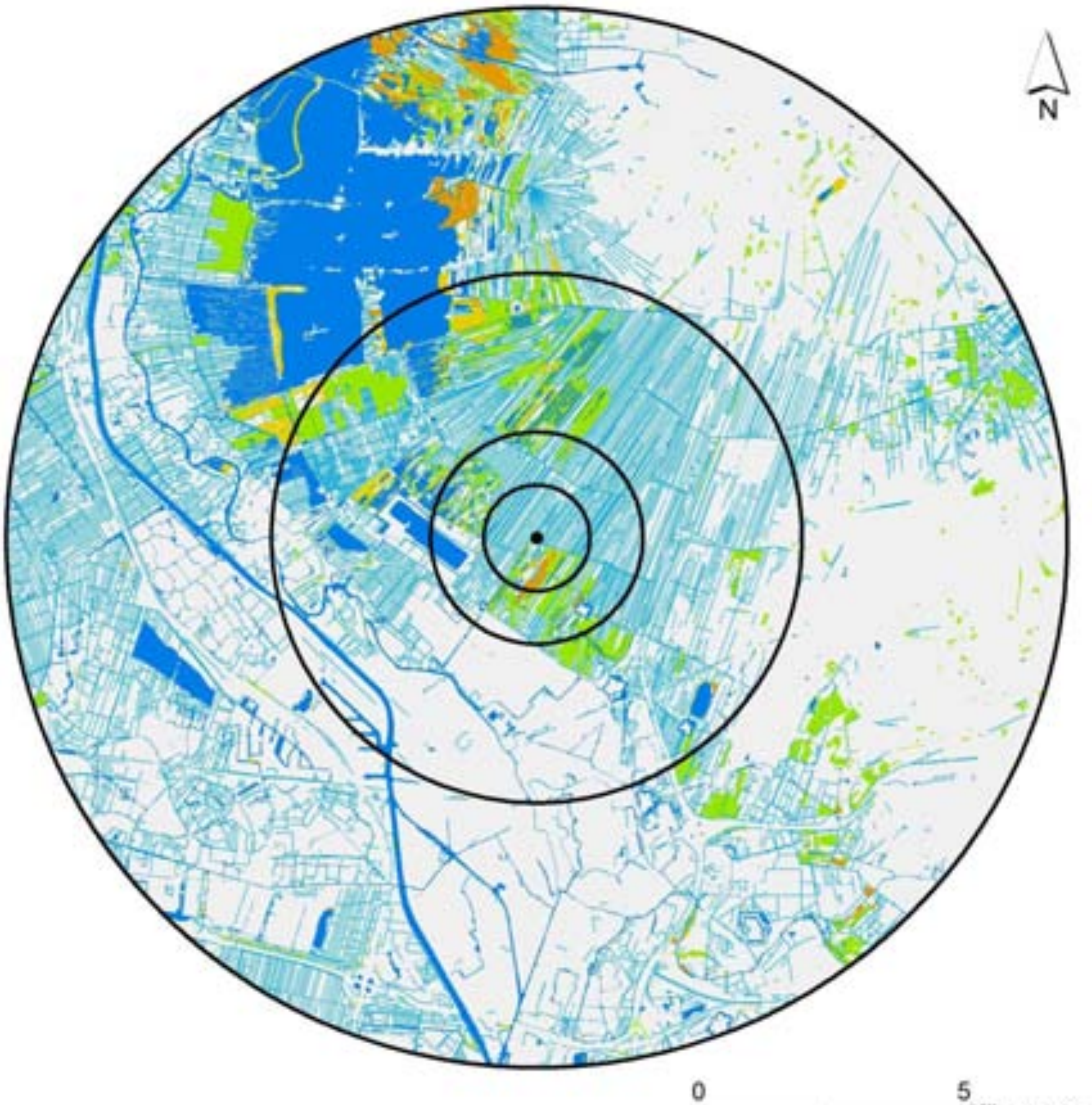

Figure A.3.4 Example of landscape buffers around a studied wetland - Molenpolder-Westbroek, the Netherlands. Each area had three landscape buffers (1km, 2km and 5km radius), centred on the centroid (black circle). The coloured patches represent habitat patches from one of the heterogeneity indices in Table 3.1. Habitat heterogeneity inside each buffer was calculated using the indices in Table 3.1.

Chapter four

Plant trait composition as an indicator for the ecological memory of rehabilitated floodplains

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Abstract

Maintaining ecosystem functioning under global change requires resilient ecosystems. Maintaining resilience is therefore a common objective for ecosystem management, but how this objective may be achieved remains largely unclear. The concept of ecological memory provides a perspective on how the adaptive capacity of ecosystems can be enhanced through management. It specifies how ecological processes in space and time assist in the reorganization of communities after disturbances. We present a trait-based approach that links environmental variables at site and patch level to plant traits. With a generalized linear mixed-effects model we test how environmental variation in management and floodplain dynamics, within and between sites, relates to plant traits that are considered relevant for ecological memory. The results show different mechanisms that intervene in ecological memory. Grazing enhances recruitment opportunities, both for internal reorganization and for colonization between sites. Dense vegetation structure selects for species survival and species ability to disperse over long distances. Hydrodynamics interact with seed dispersal mechanisms and seed persistence. We show that at different spatial levels, plant trait composition can act as an indicator of ecological processes contributing to the ecological memory of a floodplain ecosystem. For ecosystem management to maintain and use as much of this memory as possible it should incorporate measures at various levels of scale to enhance ecosystem resilience.

4.1 Introduction

Ecosystem conservation objectives are increasingly aimed at enhancing ecosystem resilience, particularly in the context of climate adaptation (Heller and Zavaleta 2009; Van Teeffelen, Vos and Opdam 2012). Ecosystems are dynamic entities, subject to variation in biotic and abiotic properties which are induced by natural and anthropogenic processes and disturbances over time (Seifan et al. 2013). The reorganization of ecosystems after disturbance, is referred to as resilience (Holling 1973). In the context of dynamic ecosystems, resilience is the magnitude of disturbance that an ecosystem can absorb before the variables and processes that control its functioning change, and move the system into another stability domain (Holling 1992). The system's resilience is partially determined by 'ecological memory', defined as the capacity of an ecosystem to maintain its structure and function after a disturbance, through reorganization of the plant community (Bengtsson et al. 2003). Ecological memory is considered to have an internal as well as an external component. The internal component supports reorganization in the area subject to disturbance, for example through survival and seed bank regeneration (e.g., Temperton and Hobbs 2004; Bischoff, Warthemann and Klotz 2009). The external component refers to a species' capacity to recolonize from surrounding areas, through dispersal (Figure 1) (Jeltsch et al. 2013). The extent to which ecological memory can facilitate resilience, is determined by (i) community processes (like competition and survival), (ii) landscape structure (like heterogeneity and patch size), and (iii) changes in (i) and (ii) over time and space (Bengtsson et al. 2003; Sun et al. 2013). The relative importance of internal and external memory will vary depending on disturbance regime and landscape structure (Bengtsson et al. 2003).

Insight in the mechanisms that influence ecological memory is fundamental to identify planning and management strategies with the aim of increasing resilience. This is of particular relevance in human-dominated landscapes, where ecosystem sites are typically small and isolated (DeAngelis and Waterhouse 1987; Standish et al. 2014). Although several studies have examined how ecological memory is encoded in site history and biological legacies, for example through seedbanks, bud banks, stem fragments and dispersal agents (Sun et al. 2013; Ortman-Ajkai et al. 2014), the degree to which these mechanisms underlying ecological memory are influenced by the relative role of internal and external memory is poorly understood. A trait-based approach can link environmental variables to plant species' traits. With the growing number of trait-based descriptions of plant strategies, we should be able to gain understanding of how communities respond to disturbances and discern which traits are important for internal and which ones for external memory (Schweiger et al. 2005; Violle et al. 2011). The advantage of using traits over species is that results are applicable beyond biogeographic borders, since species with homologous traits are expected to respond similarly to environmental filters (Keddy 1992; Sun et al. 2013; Purschke et al. 2014).

In river floodplain systems, variation in flood frequency and duration is one of the disturbances that induces environmental heterogeneity (Southwood 1988; Ortman-Ajkai et al. 2014) by destroying and generating habitats and controlling connectivity (Sedell et al. 1990; Ward and Tockner 2001; Leyer 2006). Because river floodplain systems are characterised by high patch turnover, studying such systems allow to identify changes in plant trait composition, in response to discrete flood events over considerable time frames (Wiens 2000). This makes river floodplain systems highly suitable for investigating the relative roles of internal and external memory for ecosystem resilience. This paper focusses on riparian ecosystem sites along the river Meuse in the Netherlands. We study the relation between the spatio-temporal ecosystem dynamics as captured by environmental variables, and plant traits that we hypothesized to be representative of internal and external memory. Two different spatial scales are used, the site and patch level, where patches represent homogenous areas within sites (Figure 4.1). Patch- and site-level variables relate to disturbance processes at different scales. Objectives of our study are:

1. To identify ecological processes contributing to community reorganization within and between sites.
2. To discern internal memory and external memory at different spatial scales.

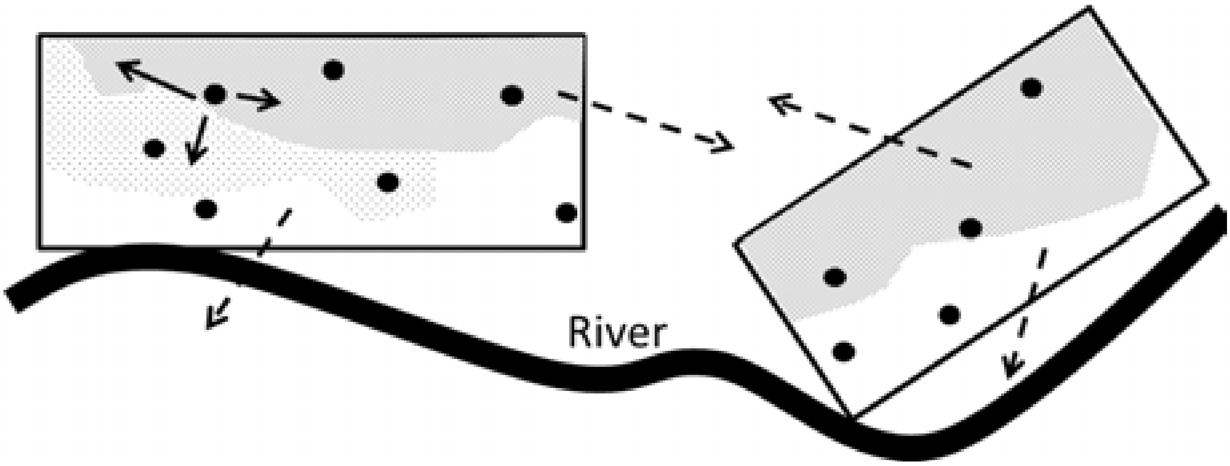


Figure 4.1. Schematic representation of rehabilitation sites (rectangles), riparian plant species monitoring sites (black circles) situated along the river (black line). The different background shading in the rehabilitation sites indicate patches that differ in habitat suitability. The solid arrows indicate the scale at which internal memory is considered to operate (within sites). The dotted arrows indicate the scale at which external memory is considered to operate (beyond sites).

4.2 Materials and methods

Study area

The River Meuse is one of Europe's large rain-fed rivers located in Northwestern Europe. The floodplain's soil and hydromorphological characteristics are specified in Van Looy et al. (2006). The Meuse is divided into six reaches based on geomorphological and hydrological characteristics. This study focusses on the section between Eijsden, at the border between Belgium and the Netherlands, and Ammerzoden in the Netherlands covering three reaches: Common Meuse, Peelhorst Meuse and Sand Meuse. This section has a total length of circa 550 km.

From 1990 onward floodplain rehabilitation has actively been pursued in several areas in the Netherlands. Floodplain rehabilitation aims at creating natural river landscapes including ecological processes, such as erosion, sedimentation, and natural grazing (Geerling et al. 2008). Our study area comprises 38 rehabilitation sites, covering 1514 ha of floodplain habitats (Figure 4.1), each with a minimum area of 5.0 ha. From these sites both riparian plant species abundance data and environmental data about abiotic conditions and management were available (described below). We consider two levels of scale in our analysis, following the hierarchical structure and related processes of floodplain systems. The upper hierarchical level is the level of the rehabilitation site including measures like natural grazing and gravel extraction. The lower hierarchical level is the level of the habitat patches within rehabilitation sites (*sensu* Tansley 1939)(Figure 4.1).

Vegetation data

Across the 38 rehabilitation sites, point abundance data were available for 125 riverine plant species that are considered indicators for a natural river system. The data were recorded once from 15,000 monitoring locations (GPS localised), in the period 2007-2009, and collected in the context of the MaasinBeeld programme (Peters and Kurstjens 2008; http://www.maasinbeeld.nl).

From the 125 recorded species we excluded aquatic species, as they are related to different environmental factors than terrestrial species (Ozinga et al. 2005), and species for which trait values were not available (trait values are described in section 'plant traits'). The final data set comprised 118 riparian plant species (Appendix 4.1). Abundance data were converted into presence-absence records to make the records comparable for statistical analyses.

Environmental data

For each rehabilitation site, two sets of environmental variables were used. The first group comprised five variables at site level (hereafter called site variables) associated to large scale ecological processes: site area in hectares excluding open water (*AreaS*), years since the start of rehabilitation (*Years*), an indicator for the rehabilitation measures taken to improve hydro-morphological processes (*Hydro*), an indicator of past gravel extraction (*Dist*), and an indicator for grazing pressure by free roaming semi-wild large herbivores (*Grazing*). The latter three variables were estimated using expert knowledge (Peters and Kurstjens 2008; http://www.maasinbeeld.nl). The second group of environmental variables comprised three variables on patch level (hereafter called patch variables) associated to small scale (hydrodynamic) processes in the landscape: patch area (*AreaP*), vegetation structure (*Veg*) and hydrodynamics (*Zone*). *Zone* combines physiological and chemical effects of flood events, like duration, depth, frequency, time of flooding, and salinity. Variables *AreaS* and *AreaP* were log transformed. Patch variables were calculated using the two-dimensional hydrodynamic river model WAQUA (Middelkoop and Perk 1998; Warmink et al. 2013; version 2008). WAQUA is calibrated and validated at the level of the vegetation patches used in this study, providing water level and flow velocities both for static and dynamic flow events. It was applied to a schematic representation of the river Meuse in the period 2004-2008 with corresponding input parameters. See Middelkoop and Perk (1998) for a detailed description.

Plant traits

The five traits that reflect a plant's capacity to locally reorganize after disturbance (internal memory) are growth form (*grform*), specific leaf area (*SLA*), seed mass (*SeedMass*) and seed bank persistence (*SeedPers*). *grform* is a classification of the way plants are morphologically adapted to unfavourable conditions (Raunkiaer 1934). *SLA* is described to relate to plants' ability to tolerate submersion due to flooding (e.g., Clevering 1997; Voesenek et al. 2006; Violle et al. 2011). Low seed mass is inherent to high seed production, contributes to the chance of successfully colonising a habitat patch (e.g., Westoby et al. 1996; Dupré and Ehrlén 2002; Violle et al. 2011) and can contribute to seed bank persistence (e.g., Nathan 2006; Ozinga et al. 2009). The traits that reflect the capacity to reorganize through spatial processes (external memory) are seed mass, as described above and via long distance dispersal, and seed dispersal by water, wind, fur, dung and birds. We consider the following dispersal vectors with a high efficiency for long-distance dispersal: water (hydrochory), wind (anemochory) and birds (endozoochory and epizoochory) (e.g., Westoby et al. 1996; Dupré and Ehrlén 2002; Ozinga et al. 2009).

Quantitative information on the traits was compiled from the trait data base LEDA (Kleyer et al. 2008). To avoid categories with very few species, the ordinal trait *grform* with eleven classes was reduced to two categories: (1) above-ground perennating buds, and (2) and below-ground perennating buds. For *SeedPers*, we classified each species according to its seed bank persistence: (1) not persistent, or (2) persistent. The quantitative traits *SLA* and *SeedMass* were log-transformed. To quantify dispersal mechanisms we classified each species into one or more dispersal agents. When a species showed memberships in multiple categories of dispersal agents, the number of trait categories was added up into the variable polychory (*poly*) and log-transformed (Appendix 4.2) (Ozinga et al. 2009).

Data analysis

The data to be analysed consist of three tables: a location * environmental data table, connected by a location * species occurrence table to a species * trait data table. For such data, the typical statistical method to use is the RLQ method (for an application see Sterk et al. 2013). However, in the present study the location * environmental data table has an hierarchical structure of sites and patches within sites, which cannot be handled in ordinary RLQ analysis. An alternative approach is the generalized linear mixed model (GLMM), as described by Jamil et al. (2013). In this approach the species occurrence is explained by traits of the species and environmental variables of the locations. It handles binary data by assuming a binomial distribution, using a logit link function to link the probability of a species occurrence to plant traits, environmental data, and their interaction. In the interaction of plant traits and environmental variables the ecological message is hidden: which plant traits modify the regression coefficients of which environmental variables? The GLMM handles pseudo-replication, both for location (multiple species per location), and species (multiple locations per species) by inclusion of random effects for location and species. The GLMM is an example of a random coefficient model, because in the random part of the model random slopes of environmental variables over species are specified. We extended the GLMM, described by Jamil et al. (2013), by inclusion of random effects not only for sites, but also for patches within sites, thereby accommodating the hierarchical structure of the location data. We used the lme4 package in R (R Development Core Team 2010) to fit the GLMM to the data. All explanatory variables were standardized, with the exception of the binary variables *grform*, *SeedPers*, and *Dist*.

In the model building phase, we applied a tiered model selection approach, modified from Jamil et al. (2012). In tier 1 we started with a null model containing only random effects for species, sites, and patches within sites, handling the pseudo-replication. Next, we added, one-by-one, species-dependent random coefficients for environmental variables to the null model, selecting variables which showed the largest improvement of Akaike’s Information Criterion (AIC) first. In this tier we selected candidate environmental variables with effects that showed random variation over species, so that potentially they interact with species traits. In tier 2, a new null model was defined as the model from tier 1 with added fixed effects for all selected environmental variables and all five plant traits. This null model served as a starting point for selection of interactions of plant traits with selected environmental variables. Next we added, one-by-one, sets of interactions of each selected environmental variable with all plant traits, selecting first the set which improved the AIC most. In tier 3, individual interactions and main effects, not involved in remaining interactions, labelled as unimportant according to AIC, were removed from the model, yielding the most parsimonious final model.

4.3 Results

All eight environmental variables were included in the first tier of the model selection process with random effects for species, sites and patches within sites. The fact that all environmental variables were selected means that plant species showed different responses (occurrences) to all environmental variables, indicating the relevance of the environmental variables for the set of species in question. The order of variable selection was *Hydro*, *Zone*, *Grazing*, *AreaS*, *Dist*, *Years*, *Veg*, *AreaP*. The second tier - with starting model containing main effects of selected environmental variables and all species traits - selected the sets of interactions of site variable *Grazing*, and patch variables *Zone* and *Veg*. In the final model, the following interactions between variables were significant (P<0.05): *SeedMass:Grazing*, *SeedPers:Zone*, *poly:Zone*, *grform:Veg* and *SLA:Veg* (Table 4.1).

Table 4.1. Effects of site and patch variables on plant traits in floodplains along the Dutch Meuse using GLMM. Parameter estimates are taken from the fixed effects of the final model based on tiered forward selection. Bolded p-values reflect statistical significance at the 0.05 level. See Appendix 4.3 for key to variable names.

Explanatory variables	Parameter estimate	Standard Error	p-Value
SeedPers:Zone	-0.21131	-2.531	<0.05
grform:Veg	0.18456	0.07677	<0.05
SeedMass:Grazing	0.18186	0.04355	<0.001
poly:Zone	-0.08795	0.03632	<0.05
SLA:Veg	0.08003	0.03630	<0.05
poly:Grazing	-0.07502	0.03961	0.06
SeedMass:Zone	0.07099	0.04004	0.08

Of these, the interactions between *SeedMass* and *Grazing*, *grform* and *Veg*, and between *SLA* and *Veg* had a positive sign (Table 4.1). The interactions between *SeedPers* and *Zone* and between *poly* and *Zone* had a negative sign. A positive interaction parameter indicates that for a unit change in the environmental variable (e.g., *Grazing*) the change in occurrence probability (on logit scale) is larger at higher trait values (e.g., *SeedMass*). These relationships are visualized in Figure 4.2.

Figure 4.2 shows for each significant interaction, how species' probabilities of occurrence change over the values of the environmental variable, predicted from the GLMM analyses. Each interaction is split for species with low, medium, or high trait values (for *SeedMass*, *poly*, and *SLA*) or binary values (for *SeedPers* and *grform*), keeping all other explanatory

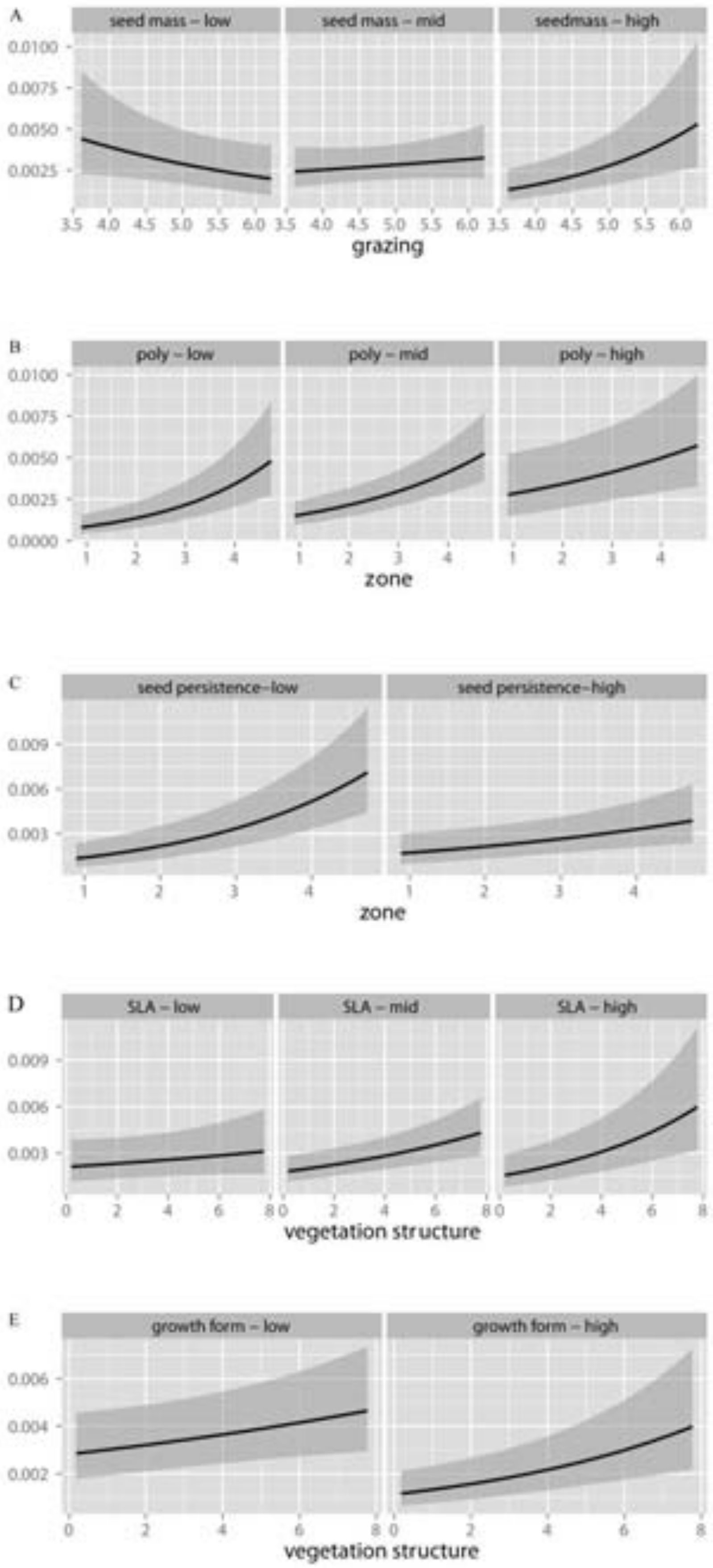


Figure 4.2. Occurrence probability of plant species (solid lines) for different classes of traits with a 95% confidence band, in relation to site or patch variables. Interactions between (A) seed mass and grazing, (B) polychory and hydrodynamic zone, (C) seed persistence and hydrodynamic zone, (D) specific leaf area and vegetation structure, and (E) growth form and vegetation structure. Based on data from floodplains along the Dutch Meuse using GLMM.

variables at their average values. The interactions quantitatively show how species are selected through environmental variables based on their traits. For example, species with a high seed mass show a positive response (higher occurrence probability) to increased grazing intensity, whereas species with a low seed mass respond negatively to increased grazing. In other words: in sites with high grazing intensity relatively more species with high seed mass are found, whereas in low grazing sites species with low seed mass dominate. For all other interactions the probability of species occurrence increases with increasing environmental value (*Zone* and *Veg*), but the rate of change differs. Plant species with a low number of dispersal mechanisms (low values of *poly*) and no seed bank persistence (low values of *SeedPers*) showed higher sensitivity to changes in the hydromorphology at the patch level (*Zone*) compared to plant species with high values of *poly* and *SeedPers*. Plant species with high *SLA* and below ground growth form showed to be more sensitive to changes in *Veg* compared to plant species with low *SLA* and above ground growth form.

4.4 Discussion

Interactions contributing to internal and external memory

The approach applied in this study allowed to extract the most relevant interactions between environmental variables and plant traits which are considered important for internal and external ecological memory in floodplains. We discuss the significant interactions here, starting with the interaction with the highest parameter value (see Table 4.1).

We found higher occurrence probability of plant species with low seed persistence in patches with high hydrodynamics. This contradicts with earlier studies indicating that in most species living in disturbed habitats have persistent seeds (Ackerly 2004). Though, work on large datasets showed that a collection of variables, including seed shape, ease of burial and physiological traits influences seed persistence (Thompson et al. 1998). Our results seems in accordance with studies showing that pioneer plant species are adapted to high dynamic environments and do not invest in seed persistence (Amoros and Bornette 2002; Ozinga et al. 2009; Casanova 2015). In contrast, species adapted to low dynamic environments have to invest in seed persistence to survive on the long term, thus relying on internal memory. Taken together, internal memory is the major driver in less dynamic floodplain zones, whereas external memory dominates highly dynamic floodplains.

The higher occurrence probability of species with an above ground budbank in dense vegetation indicates the abundance of endurers. Endurers are one of the adaptation strategies described by Naiman and Decamps (1997). Those strategies (avoiders, invaders, resisters and endurers) are useful to understand species adaptation to flooding. Endurers resprouts after breakage or burial of either the stem or roots from floods. High occurrence probability of endurers can promote short distance dispersal with flooding as above-ground connections are easily able to anchor in the soil through adventious roots, which are characteristic of flood-tolerant plant species (Boedeltje et al. 2003). Therefore, functional adaptation of these species indicates a positive contribution of the above ground budbank to the internal memory of the ecosystem.

Our results show a positive interaction between seed mass and grazing of the sites. Seed mass is probably the most important characteristic of a plant species with regard to seedling recruitment (Leishman, Westoby and Jurado 1995; Coomes and Grubb 2003; Turnbull et al. 2004). Large seeds are better sustained by nutrients and superior buoyant in water favouring long-distance dispersal (Römermann, Tackenberg and Poschlod 2005; Leyer 2006). The relationship between seed mass and grazing by free roaming ‘semi-wild’ herbivores is relatively poorly studied though. One study including low-intensity permanent grazing with free-ranging cattle, sheep and ponies, showed that large seeds germinated better in the presence of herbivores then in abandoned areas compared to small seeds (Kahmen and Poschlod 2007). Since the herbivores in our study are free-ranging in a site, some areas are intensively grazed and others are barely grazed. Grazed areas are characterized by gradients of bare soil through trampling, regenerating vegetation and mature vegetation. The positive effects of gaps in enhancing seedling recruitment is widely acknowledged (e.g., Leemans 1991; Zobel et al. 2000). In this way grazing promotes the internal and external memory of floodplain plant species by creating suitable habitats for internal reorganization and contributing to colonization of previously disturbed sites.

Plant species with low polychory (fewer dispersal vectors) showed to be more sensitive to changes in hydrodynamics compared to plant species with high polychory (more dispersal vectors). Hydrodynamics is a combination of physiological and chemical water influences, like duration, depth, frequency and time of flooding, and salinity. This variable is often used as an indicator of river-floodplain connectivity (Boedeltje et al. 2003; Leyer 2006). These studies show high number of water-dispersed seeds in frequently disturbed habitats, and indicate the low importance of wind and animal dispersal in these areas. The results suggests increased importance of investment in colonization of new patches (external memory) relative to short-distance dispersal and local persistence. However, in this study dispersal vectors are not analysed separately because the amount of data that can be processed with a GLMM is limited.

The significant positive effect of the vegetation structure on the specific leaf area of plant species at patch level is consistent with the hypothesis that species in less disturbed floodplain habitats invest more in their potential relative growth rate. These species are also known for their shade-tolerance and resource-rich environments (Cornelissen et al. 2003). As disturbance frequency decreases, biological interactions increase (e.g., competition and herbivory), favouring competitive species. Disturbances by floods no longer dominate plant communities at this end of the gradient. This shows that species living in dense vegetation structures rely on internal memory of the ecosystem for reorganisation.

Importance of scale for ecosystem management

Our study showed that species traits can be explained by a GLMM that incorporates environmental gradients of disturbances on site and patch level. Scale is essential to the analysis of ecological processes (Holling 1992). The relationship between two variables in a natural system can be obscured by other variables at other scales and the interferences drawn from an observed relationship can be distorted or even reversed depending on the scale at which that relationship is measured. Van Looy et al. (2006) found that the taxonomic and functional structure of floodplain meadow communities was distinct among ecoregions and that clustering of species by ecoregion reflected different species' affinities for environmental variables. Relationships between species traits and environmental gradients provide information about environmental filtering, particularly when the traits suggest an advantage in the associated environment (e.g., Keddy 1992; Schweiger et al. 2005). The use of internal and external memory appeared to be a suitable way to distinguish ecological processes at various spatial and temporal scales. Our study shows that environment-trait relationships relevant for the adaptive capacity are found at both site and patch level. In a rapidly changing world, those results can be used to adjust landscape structure and disturbance regimes, where possible, to develop resilient floodplain ecosystems.

4.5 Conclusions

We found that environmental variables associated with floodplain disturbances were significantly related with plant traits at two spatial scale levels. At site level grazing pressure is significantly related with seed mass. At patch level hydrodynamics is significantly related with polychory and seed persistence, and vegetation structure with specific leaf area and growth form. We linked these significant relationships to ecological processes that allow ecosystems to reorganise following disturbances: internal and external ecological memory. By better understanding how environmental processes filter species and shape communities based on traits, the capacity of these systems to reorganise after disturbances can be better managed, in favour of ecological resilience. Our trait-based approach contributes to understand phenomena that can be used to predict vegetation responses to disturbances around the world. GLMM's are useful tools in this respect, allowing to obtain a better understanding of the relative role of ecological processes at different spatial scales and ultimately reinforcing management strategies to support ecological resilience.

Appendix 4.1

Table A.4.1 Plant species included in the study.

Name_species	Code_species
Agrimonia eupatoria	Agr_eup
Agrimonia procera	Agr_pro
Ajuga reptans	Aju_rep
Allium oleraceum	All_ole
Allium scorodoprasum	All_sco
Anthemis tinctoria	Ant_tin
Anthyllis vulneraria	Ant_vul
Aphanes arvensis	Aph_arv
Arabis hirsuta subsp. hirsuta	Ara_hir
Arctium tomentosum	Arc_tom
Aristolochia clematitis	Ari_cle
Armoracia rusticana	Arm_rus
Artemisia absinthium	Art_abs
Arum maculatum	Aru_mac
Astragalus glycyphyllos	Ast_gly
Ballota nigra	Bal_nig
Berteroa incana	Ber_inc
Brachypodium sylvaticum	Bra_syl
Bromopsis inermis subsp. inermis	Bro_ine
Caltha palustris	Cal_pal
Campanula rapunculus	Cam_rap
Cardamine amara	Car_ama
Carex caryophyllea	Car_car
Cardamine impatiens	Car_imp
Carex remota	Car_rem
Centaurea cyanus	Cen_cya
Centaurium erythraea	Cen_ery
Centaurium pulchellum	Cen_pul
Centaurea scabiosa	Cen_sca
Chrysosplenium oppositifolium	Chr_opp
Circaea lutetiana	Cir_lut
Clinopodium vulgare	Cli_vul
Colchicum autumnale	Col_aut
Conium maculatum	Con_mac
Cruciata laevipes	Cru_lae
Cymbalaria muralis	Cym_mur
Cynosurus cristatus	Cyn_cri
Cyperus fuscus	Cyp_fus
Dianthus armeria	Dia_arm

Dianthus deltoides	Dia_del
Digitalis purpurea	Dig_pup
Dipsacus pilosus	Dip_pil
Echinops sphaerocephalus	Ech_sph
Eleocharis ovata	Ele_ova
Elymus caninus	Ely_can
Equisetum hyemale	Equ_hye
Erigeron annuus	Eri_ann
Euphorbia seguieriana	Eup_seg
Filago vulgaris	Fil_vul
Fragaria vesca	Fra_ves
Geranium columbinum	Ger_col
Geranium pratense	Ger_pra
Geranium pyrenaicum	Ger_pyr
Geranium rotundifolium	Ger_rot
Helictotrichon pubescens	Hel_pub
Hieracium amplexicaule	Hie_amp
Hordeum secalinum	Hor_sec
Hypericum hirsutum	Hyp_hir
Inula britannica	Inu_bri
Kickxia elatine	Kic_ela
Knautia arvensis	Kna_arv
Lathyrus nissolia	Lat_nis
Leersia oryzoides	Lee_ory
Leonurus cardiaca	Leo_car
Leontodon hispidus	Leo_his
Lepidium draba	Lep_dra
Lepidium latifolium	Lep_lat
Limosella aquatica	Lim_aqu
Lythrum portula	Lyt_por
Malva alcea	Mal_alc
Medicago falcata	Med_fal
Medicago polymorpha	Med_pol
Mentha longifolia	Men_lon
Mentha x rotundifolia	Men_rot
Mentha suaveolens	Men_sua
Odontites vernus subsp. serotinus	Odo_ver
Ononis repens subsp. spinosa	Ono_rep
Origanum vulgare	Ori_vul
Orobanche minor	Oro_min
Parietaria judaica	Par_jud
Parietaria officinalis	Par_off
Persicaria bistorta	Per_bis
Peucedanum carvifolia	Peu_car

Picris echioides	Pic_ech
Plantago arenaria	Pla_are
Plantago media	Pla_med
Potentilla argentea	Pot_arg
Potentilla verna	Pot_ver
Primula veris	Pri_ver
Ranunculus sardous	Ran_sar
Rhinanthus alectorolophus	Rhi_ale
Rhinanthus minor	Rhi_min
Rumex thyrsiflorus	Rum_thy
Salvia pratensis	Sal_pra
Sambucus ebulus	Sam_ebu
Sanguisorba minor	San_min
Sanguisorba officinalis	San_off
Saxifraga granulata	Sax_gra
Saxifraga tridactylites	Sax_tri
Scirpus sylvaticus	Sci_syl
Securigera varia	Sec_var
Sedum album	Sed_alb
Sedum reflexum	Sed_ref
Sedum sexangulare	Sed_sex
Silene vulgaris	Sil_vul
Sisymbrium austriacum (subsp. chrysanthum)	Sym_lan
Thymus pulegioides	Thy_pul
Trifolium fragiferum	Tri_fra
Trifolium striatum	Tri_str
Trisetum flavescens	Tri_fla
Ulmus laevis	Ulm_lae
Verbascum blattaria	Ver_bla
Verbena officinalis	Ver_off
Veronica austriaca subsp. teucrium	Ver_aus
Veronica scutellata	Ver_scu
Vicia lathyroides	Vic_lat
Viola odorata	Vio_odo
Vulpia bromoides	Vul_bro

Appendix 4.2

Table A.4.2. Plant traits used in the analyses. Codes refer to Appendix 4.1.

Code_species	Growthform	SLA Median	SeedMass	Persistentseed	Wind/animal	Water
Agr_eup	Hemicryptophyte	17.675	15.969	0	1	1
Agr_pro	Hemicryptophyte	19.4	9.79	0	1	0
Aju_rep	Hemicryptophyte	32	1.459	1	0	0
All_ole	Geophyte	11.8	2.906	0	0	0
All_sco	Geophyte	4.65	1.17	0	0	0
Ant_tin	Therophyte	31.22	0.22481	1	1	0
Ant_vul	Hemicryptophyte	15.9	4.872	0	1	0
Aph_arv	Therophyte	17	0.162	1	1	0
Ara_hir	Hemicryptophyte	26.9	0.105	1	0	1
Arc_tom	Hemicryptophyte	50	14.8	1	1	0
Ari_cle	Hemicryptophyte	16.885	32.43675	0	0	1
Arm_rus	Geophyte	19.4	2.562552	0	0	1
Art_abs	Hemicryptophyte	26.7	0.107	1	1	0
Aru_mac	Geophyte	33.1	31.925	0	0	0
Ast_gly	Hemicryptophyte	25.8	5.175	0	1	0
Bal_nig	Hemicryptophyte	21.25	0.856	1	1	0
Ber_inc	Therophyte	19.95	0.655	1	0	0
Bra_syl	Hemicryptophyte	41.32	3.122	0	1	0
Bro_ine	Geophyte	22.415	3.672	0	1	0
Cal_pal	Hemicryptophyte	27.3	1.062	0	0	1
Cam_rap	Hemicryptophyte	39.91	0.04	0	1	0
Car_ama	Hemicryptophyte	44.15	0.256	1	0	0
Car_car	Geophyte	21.3	1.417	0	0	1
Car_imp	Therophyte	33.8	0.267	1	0	0
Car_rem	Hemicryptophyte	25.75	0.377	1	1	1
Cen_cya	Therophyte	21.06	4.825	1	1	0
Cen_ery	Hemicryptophyte	19.68	6.697	0	1	0
Cen_pul	Hemicryptophyte	22.54	0.012	1	1	0
Cen_sca	Therophyte	43.2	0.012	1	0	0
Chr_opp	Hemicryptophyte	23.35	0.065	0	0	0
Cir_lut	Geophyte	36.7	1.719	0	1	0
Cli_vul	Hemicryptophyte	23.6	0.427	1	1	0
Col_aut	Geophyte	21.91	5.488	0	0	1
Con_mac	Therophyte	24.5	2.385	1	0	0
Cru_lae	Hemicryptophyte	25.87	5.34	0	1	0

Cym_mur	Chamaephyte	23.4	0.107	0	0	0
Cyn_cri	Hemicryptophyte	22.7	0.596	0	1	1
Cyp_fus	Therophyte	41.61	0.048	1	1	1
Dia_arm	Hemicryptophyte	14.88	0.238	0	0	0
Dia_del	Chamaephyte	16.05	0.199	0	0	0
Dig_pup	Hemicryptophyte	17.3	0.07	1	0	0
Dip_pil	Hemicryptophyte	55.05	5.577	0	1	0
Ech_sph	Hemicryptophyte	50	22.6	1	1	0
Ele_ova	Therophyte	2.5	0.107	1	1	0
Ely_can	Hemicryptophyte	27.85	4.59	0	1	0
Equ_hye	Geophyte	2.88	0.05	0	1	0
Eri_ann	Hemicryptophyte	28.065	0.07	1	1	0
Eup_seg	Hemicryptophyte	18.4	0.88	1	0	0
Fil_vul	Therophyte	26.5	0.076	0	0	0
Fra_ves	Hemicryptophyte	19.7	0.313	1	1	0
Ger_col	Therophyte	27.45	3.146	1	1	0
Ger_pra	Hemicryptophyte	21.35	8.637	1	1	0
Ger_pyr	Hemicryptophyte	28.03	1.545	0	1	0
Ger_rot	Therophyte	24	1.3892	0	1	0
Hel_pub	Hemicryptophyte	22.37	1.991	0	1	0
Hie_amp	Hemicryptophyte	29.19	0.78	0	1	0
Hor_sec	Hemicryptophyte	32.1	3.844	0	1	1
Hyp_hir	Hemicryptophyte	27.2	0.6	1	0	0
Inu_bri	Hemicryptophyte	20.16	0.0825	1	1	0
Kic_ela	Therophyte	40.3	0.367	1	0	0
Kna_arv	Hemicryptophyte	18.72	4.077	0	1	0
Lat_nis	Therophyte	19.9	7.492	0	0	0
Lee_ory	Hydrophyte	10	1.254	1	1	1
Leo_car	Hemicryptophyte	15	0.885	0	1	0
Leo_his	Hemicryptophyte	24.64425	1.061	0	1	0
Lep_dra	Geophyte	21.05	1.588	1	0	0
Lep_lat	Hemicryptophyte	15.31	2.354	1	0	0
Lim_aqu	Therophyte	27.3	0.016	1	0	0
Lyt_por	Therophyte	24	0.036	1	0	0
Mal_alc	Hemicryptophyte	28.14	3.9	1	1	0
Med_fal	Hemicryptophyte	18.1	1.74	0	1	0
Med_pol	Therophyte	20.125	2.83	1	1	0
Men_lon	Hemicryptophyte	28.635	0.058	0	1	0
Men_rot	Hemicryptophyte	27	0.01	0	1	0
Men_sua	Hemicryptophyte	27.4	0.046	0	1	0
Odo_ver	Therophyte	15.2	2.562552	1	0	0
Ono_rep	Chamaephyte	28.41	6.079	0	0	0
Ori_vul	Chamaephyte	21.1959	0.102	1	0	0
Oro_min	Semi-parasite	5	0.02545	1	1	0

Par_jud	Hemicryptophyte	34.9	0.141	1	0	0
Par_off	Hemicryptophyte	60.79	0.39	1	0	0
Per_bis	Geophyte	26.44	5.48	0	0	1
Peu_car	Hemicryptophyte	12	2.228	0	0	1
Pic_ech	Therophyte	31.8	0.69	0	0	1
Pla_are	Therophyte	16.705	1.06	1	1	0
Pla_med	Hemicryptophyte	19.55	0.446	0	1	0
Pot_arg	Hemicryptophyte	16.7	0.116	1	1	0
Pot_ver	Hemicryptophyte	11.4	0.621	1	1	0
Pri_ver	Hemicryptophyte	17.45	0.82	0	0	0
Ran_sar	Therophyte	34.41	1.437	1	0	0
Rhi_ale	Semi-parasite	21.18	4.82	1	0	1
Rhi_min	Semi-parasite	19.945	2.803	0	0	1
Rum_thy	Hemicryptophyte	20.43	0.818	1	1	0
Sal_pra	Hemicryptophyte	26.38	2.594	0	1	1
Sam_ebu	Hemicryptophyte	19.995	9.5346	1	1	0
San_min	Hemicryptophyte	19.25	4.106	0	1	1
San_off	Hemicryptophyte	21.4	2.616	0	0	1
Sax_gra	Hemicryptophyte	30.8	0.043	1	0	1
Sax_tri	Therophyte	23.07	0.015	1	0	1
Sci_syl	Geophyte	20.65	0.13	0	1	1
Sec_var	Hemicryptophyte	28.49	6.98	0	0	0
Sed_alb	Chamaephyte	15.08	0.02	0	0	0
Sed_ref	Chamaephyte	10.7	0.074	0	0	0
Sed_sex	Chamaephyte	13.98	0.01	1	1	0
Sil_vul	Hemicryptophyte	18.85	1.033	1	1	0
Sym_lan	Hemicryptophyte	15	0.04	0	1	1
Thy_pul	Chamaephyte	26.56	0.167	0	1	0
Tri_fra	Hemicryptophyte	24.865	1.303	0	1	1
Tri_str	Therophyte	20.02	1.303	0	1	1
Tri_fla	Hemicryptophyte	20.8	0.423	0	1	1
Ulm_lae	Phanerophyte	43.42	8	0	1	0
Ver_bla	Hemicryptophyte	30	0.11	1	0	0
Ver_off	Hemicryptophyte	14.2	0.415	1	1	0
Ver_aus	Chamaephyte	22.47	0.18	0	1	1
Ver_scu	Hemicryptophyte	31.58889	1.238	1	1	0
Vic_lat	Therophyte	25.8	2.008	1	0	0
Vio_odo	Hemicryptophyte	29.35	1.73	1	0	0
Vul_bro	Therophyte	23.5	0.421	0	1	0

Chapter 5

Using the ecological memory concept to assess how management can enhance ecosystem resilience

Marjolein Sterk, Marleen Cobben and Peter Schippers

Abstract

Maintaining ecosystem functions under global change requires resilient ecosystems. In intensively-used landscapes, ecosystems often occur in small and isolated fragments, reducing their adaptive capacity to changes. Increasing the resilience of such systems is a common conservation objective, but how such objectives may be achieved remains largely unclear. The concept of ecological memory provides a perspective on how the adaptive capacity of ecosystems can be enhanced through management. We adopt four plant strategies – avoiders, invaders, resisters and endurers - classified by their adaptation to flooding. With a spatially explicit model of a floodplain ecosystem we identify those strategies most vulnerable to variation in landscape heterogeneity and/or flooding regime. Our results show how disturbance and heterogeneity can interact to select for particular strategies, and what level of heterogeneity is preferred under expected flooding regimes when managing for resilient ecosystems. The results show that the abundances of all plant strategies are preserved with low landscape heterogeneity and one flood per year, whereas a higher heterogeneity or a lower flood frequency resulted in a loss of strategy types. These results illustrate that reorganization after a flood is dependent on the ecological memory. The strategies relying on an internal memory profit from large aggregated clusters whereas strategies that contribute to the external memory survive in any landscape. Our results confirm the suggestion that to maintain resilience in ecosystems managers need to incorporate disturbed areas and the surrounding landscape.

5.1 Introduction

Natural disturbance regimes are expected to change under increasing global and regional environmental pressures and this will potentially affect ecosystems (Renton et al. 2012; Milner et al. 2012; Zhang et al. 2015) through shifts in community composition and diversity, and ecosystem structure and functioning (de Bello et al. 2010; Dainese et al. 2014; Perry et al. 2015). The response of ecosystems to change is a central theme in the ecological resilience concept (Spears et al. 2015). Resilience is defined as the capacity of an ecosystem to absorb disturbances, reorganize and maintain its adaptive capacity (Carpenter et al. 2001, Gunderson 2000). Such adaptive capacity is related to biodiversity, implying that resilient ecosystems contain sufficiently large numbers of species with similar functions. Diversity is also determined by spatial heterogeneity (Peterson 2002; Opdam et al. 2003; Schippers et al. 2015)) through processes at different spatial scales related to persistence, dispersal and establishment of species. These processes define ecological memory (Bengtsson et al. 2003), which is divided in the internal memory (within a habitat) and the external memory (between habitats) and depends on the functioning of three interacting species groups: biological legacies (species, or their structures, persisting in a disturbed habitat); mobile links (species, or their structures, dispersing through the landscape); and support organisms (species remaining in undisturbed habitats as sources to colonize disturbed habitats) (Nyström and Folke, 2001; Bengtsson et al. 2003; Garćia et al. 2013). These different groups imply that habitats with a relatively large internal memory ensure rapid reorganization. As spatial heterogeneity increases and the suitable habitat patches become smaller, the internal memory will be insufficient for rapid reorganization and the ecological memory will be relatively more dependent on the external memory. In a highly fragmented landscape the external memory will be insufficient. This leads to slow reorganization and thus reduced resilience.

River floods are well-studied disturbances in floodplains and are part of environmental variability driving ecological processes and biodiversity (Wolfert et al. 2002). Changes in flood regimes as projected under global change (Tockner and Stanford, 2002; Perry et al. 2015) are therefore expected to change floodplain ecosystems. This implies that restoration of the original ecosystems and its community is not necessarily the most effective approach to manage floodplains (Moreno-Mateos et al. 2012). Floodplain heterogeneity (i.e. the distribution of flooded habitat) is expected to affect reorganization after disturbance in various ways (Van Teeffelen et al. 2012; Ortmann-Ajkai et al. 2014). Direct effects of flooding include: (1) plant breakage or mortality, thereby selecting species that are better adapted to flooding; (2) transport and deposition of seeds (Jansson *et al*. 2000, 2005; Goodson *et al*. 2003); and (3) creation of new patches for colonization, thereby facilitating new establishments. These all result in potential shifts in plant community composition and diversity, and ecosystem structure and function. The mechanisms and plasticity of plant species to respond to flooding vary greatly, being largely species-specific and reflective of suitable habitat along the riparian elevation gradient (Grime, 1997; Naiman and Décamps, 1997; van Eck *et al*. 2004; Leyer, 2006). These responses depend on inherited and species specific traits (Hobbs and Yates 2003; Henle et al. 2004; Ewers and Didham 2006; Gaudes et al., 2010), which are assumed to represent evolutionary adaptations to the physical and biological environment of a plant species. The relationship between habitat disturbance and plant traits have been an active research field for decades (e.g., Weiher et al. 1999; Schippers et al. 2001; Gerisch et al. 2012), but whether the identified traits alone can effectively explain species responses, is still debated (Arthaud et al. 2011; Kraft et al. 2015; McCune and Vellend, 2015).

Despite the above findings little is known about the interacting effects of plant traits, floodplain heterogeneity and flooding regime on the ecological memory of the ecosystem. Here we explore the spatio-temporal variability in plant species responses to changing flood frequency, along a gradient of floodplain heterogeneity. For this we adopt four plant strategies classified by their adaptation to flooding: avoiders, invaders, resisters and endurers (Naiman and Décamp 1997; Naiman et al. 1997). These strategies represent the range of persistence, dispersal and establishment characteristics available in floodplain ecosystems. Their relative contributions to the internal and external memory differ. We chose temperate floodplains along a rain fed river in north Western Europe, as our reference system for the strategy definitions. We interpret variation in the relative abundances of strategies as a change in the ecological memory with, ultimately, effects on plant establishment. With a spatially explicit model of a floodplain ecosystem we address the following questions:

1. How does the relative abundance of plant strategies vary under a changing flooding regime?
2. How does relative abundance of plant strategies vary along a heterogeneity gradient?
3. Do flooding-heterogeneity interactions affect these strategies' abundances?

In addressing these questions, we aim to identify those strategies most vulnerable to variation in heterogeneity and/or flooding regime. Our results show how disturbance and heterogeneity can interact to select for particular strategies, and what level of heterogeneity is preferred under expected flooding regimes when managing for resilient ecosystems.

5.2 Materials and methods

For this study we used TRANSPOP, a spatially explicit demographic model for vegetation dynamics (Schippers et al. 2001). The model is developed to simulate competition among individuals with different adult longevity, seed longevity and seed mass in relation to environmental disturbance. In our model disturbance is specified as flooding. We extended the model with landscape heterogeneity, modelled as different aggregated areas of non-flooded sites in a flooded landscape.

Landscape

The spatially explicit structure is represented by a grid where each individual cell represents a site of 10 x 10 cm in which a single strategy can establish, die and reproduce. Besides one adult, each cell can contain an unlimited number of seeds from the strategies present in the vegetation. The total grid size is 600 x 600 cells, i.e. 60 x 60 m. To avoid edge effects the grid space is modelled with periodic boundary conditions for simulating a large (infinite) system.

Demographic structure

For vascular plants, the temperate climatic zone is characterised by seasonal changes. In this model, species produce seeds to disperse at the end of each growing season. Some seeds germinate in spring while others die or are dormant in the soil. Seeds germinate only in vegetation gaps and seeds of different strategies compete for the open site. Open sites are created in late summer by the natural mortality of adults or in the winter by flooding.

The processes described above are summarized in the demographic structure of the model (Figure 5.1). The state variables are the number of seeds (*Seeds*) and the number of plants (*Plants*). This gives the model a simple dynamic structure including five transitions: (1) seed production by an adult in late summer N_s; (2) the probability that an adult will survive during the winter P_a; (3) the probability that an adult will persist flooding in late winter D_a; (4) the probability that a seed will outcompete the other seeds and become an adult during spring C_s; and (5) fraction of seeds that survive through the year P_s. The transitions are dependent on the species' strategy (see below).

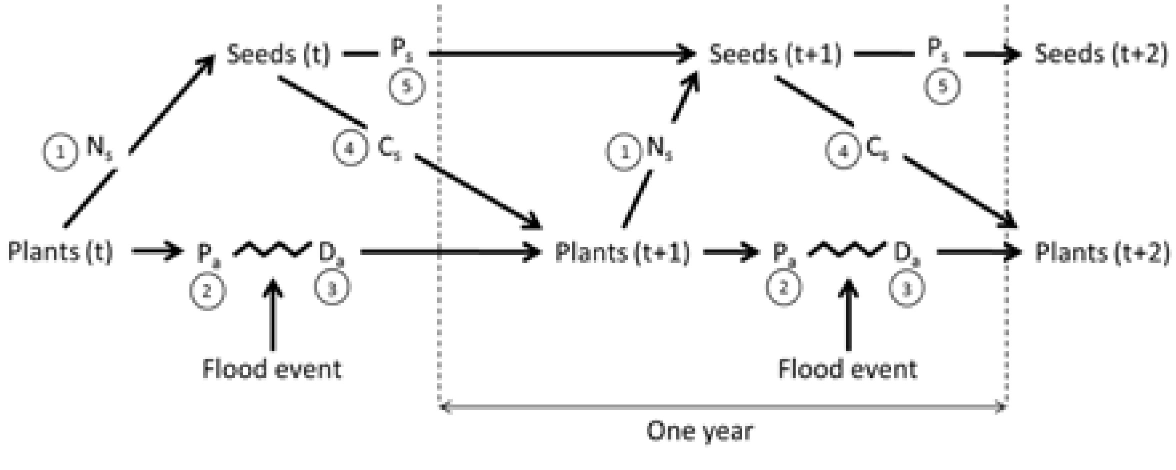


Figure 5.1. Plant life cycle transition scheme of the model per time step. P_a, D_a, P_s, C_s and N_s are the transition processes for respectively, natural adult survival, adult survival after flooding, seed persistence, germination and seed dispersal. The numbers refer to the sequence of events in a one-year cycle. For each individual: (1) Flowering and dispersal of seeds in late summer; (2) Natural adult survival in winter; (3) Adult survival after

flooding in late winter; (4) Germination of seeds in spring; and (5) Natural survival of dormant seeds through the year.

In the model one site can contain only one adult. Therefore adult recruitment C_s is modelled with a lottery processes (Lavorel and Chesson 1995). The probability that a seed of a strategy will become adult is determined by the number of available seeds.

Flooding

We model a floodplain where 50% of the sites can be flooded and 50% of the sites will never be flooded. Additionally, the non-flooded sites are randomly clustered to change the heterogeneity of the landscape. The size of the clusters vary and the smaller the clusters, the higher the landscape heterogeneity. The sensitivity of an adult plant for flooding represents the probability that a plant dies when flooded, for example, if the sensitivity is 0.8 the adult plant has 80% chance that it dies due to a flooding event (Table 5.1).

Table 5.1 Species parameters of four plant strategies typical for floodplain ecosystems used in the model.

Strategy	Avoiders	Invaders	Resisters	Endurers	Literature
Adult survival (year^{-1})	0.8	0.0	0.8	0.8	Schippers *et al.* (2001)
Adult sensitivity to flooding (event^{-1})	1.0	1.0	0.2	0.0	Naiman and Décamp (1997)
Seed production (site^{-1})	2000	3000	800	500	Kleyer *et al.* (2008)
Seed survival (year^{-1})	0.0	0.5	0.5	0.5	Kleyer *et al.* (2008)

Plant strategies in floodplains

We adjusted the eight plant strategies parameterized by Schippers et al. (2001) to four plant strategies adapted to flooding:

1. **Avoiders** lack adaptation to flooding and have an average number of seeds to be dispersed by wind or animals. As no flooding occurs in their site, adult longevity tends to evolve high values in order to obtain more time for reproduction.
2. **Invaders** lack adaptation to flooding and produce high numbers of wind or water-disseminated seeds. Frequent flooding forces them to spend a minimum share of their lifetime to individual growth, i.e. leading to low adult longevity.
3. **Resisters** can withstand flooding for weeks and produce a relative low number of seeds that can be dispersed by any dispersal factor. Due to the harsh conditions, only high values of longevity may grant enough time to complete a life cycle.

4. **Endurers** resprout after breakage or burial of either the stem or roots by floods.Vegetative parts are low in number and dispersed by water. They also produce a low number of seeds.

Flooding tends to select for high longevity to grant enough time to run through a complete life cycle (strategy description by, for example, Naiman and Décamp, 1997; Naiman et al. 1997; Camporeale et al. 2013). For additional species parameters we adopted a dataset of vascular plant species in river meadows categorized into the four strategies (Van Looy et al. 2006) and we used these species to screen the LEDA database for parameter values (Kleyer et al. 2008). Table 5.1 gives an overview of species demographic parameters used in the model. How the different dispersal strategies of avoiders, resisters and endurers effect the probability of seed arrival in a site is shown in Figure 5.2. Their seeds were distributed according to a negative exponential distribution (Schippers et al. 2001). Since the landscape available within our model is small compared to the dispersal distance of the well-dispersing seeds of the invader, those seeds were allowed to disperse homogeneously over the whole landscape with an arrival probability of 1/360,000.

In terms of ecological memory the four strategies have different functions that all affect the internal and external memory (Bornette et al. 2008). An avoider only survives in non-flooded sites and produces many seeds to colonize sites at relative short distance (Figure 5.2). The avoider does not invest in a seedbank. Therefore, avoiders need non-flooded sites to survive as an adult to fulfil their role as supporting organism to recolonize flooded sites. In contrast, the invader does not invest in adult survival but produces many seeds to be dispersed over long distances. Moreover, invaders have a persistent seedbank and need flooding to create open sites for germination. Resisters and endurers are not (very) sensitive to flooding and produce relative low seed numbers. In contrast, resisters disperse their seeds over long distances increasing the chance to colonise open sites for germination (Figure 5.2). Endurers persist in flooded sites and disperse their seeds over relative short distances (Figure 5.2). Therefore the endurers’ chance to colonise open sites is smaller compared to the resister. But the number of seeds per site, the seedbank, can be higher.

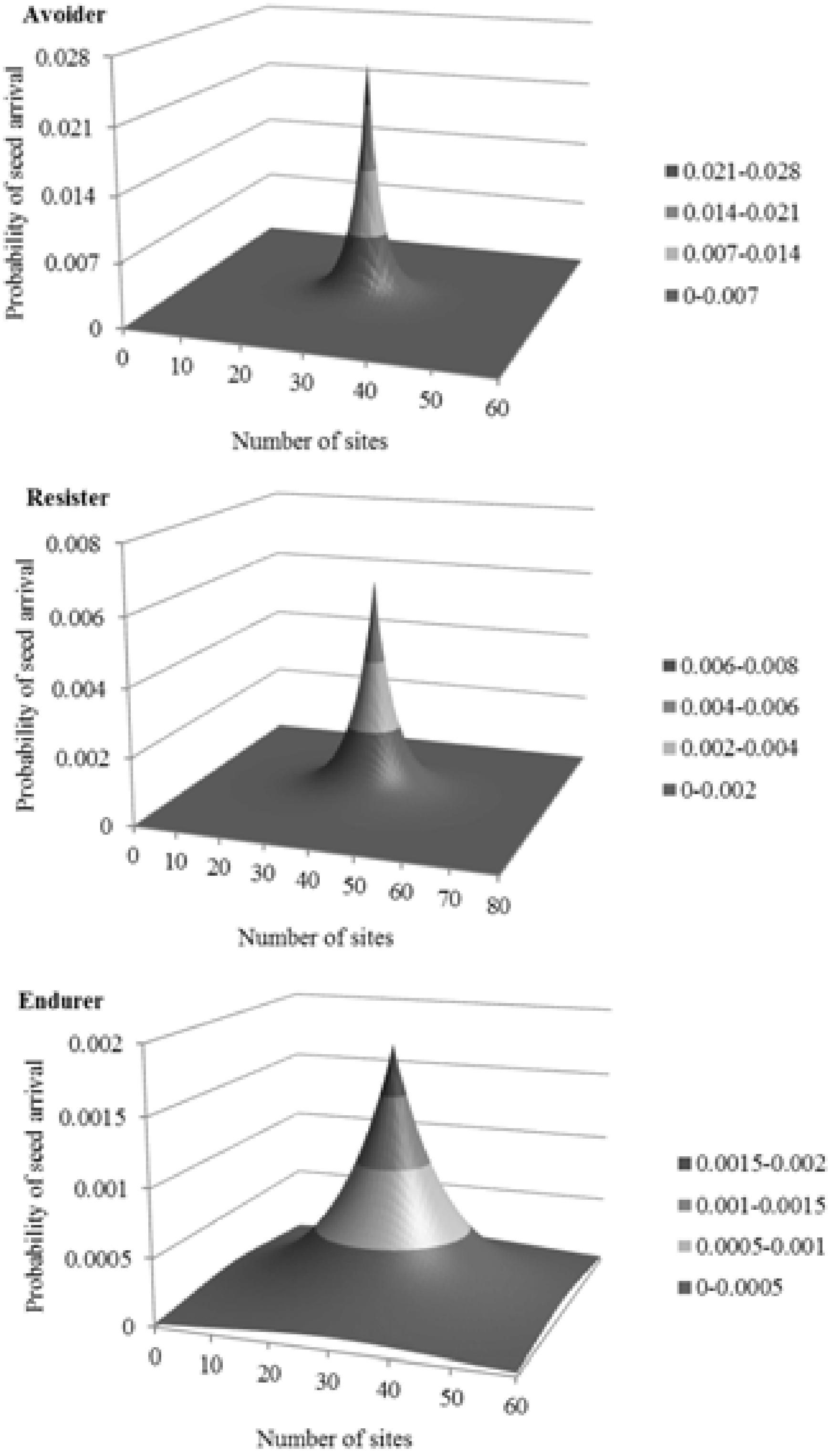


Figure 5.2. Probability of seed arrival in a site for avoiders, resisters and endurers. The seeds were distributed according to a negative exponential distribution. Seeds of the invader were allowed to disperse homogeneously over the whole landscape with an arrival probability of 1/360,000 and are not shown (Schippers et al. 2001). Note that the x-axes and y-axes scales differ.

Initialisation

The parameterisation as described in Appendix 5.1, with one flood per year and heterogeneity with 2000 non-flooded sites aggregated, is termed the ‘reference situation’. Each simulation started with the four strategies randomly distributed over the sites. All strategies were present in an equal number of sites. The first process is seed production followed by other transition processes as described in Figure 5.1.

Simulation experiments

We subjected the plant strategies to four flooding scenarios with a probability of one flooding per 1 year, per 2 years, per 3 years or per 4 years under constant landscape heterogeneity. In the second experiment, the strategies were subjected to five different landscape heterogeneity scenarios under constant flooding regime. The total number of 180,000 not-flooded sites were aggregated in clusters of 100, 200, 500, 1000 or 2000 sites (respectively 1, 2, 5, 10 or 20 m^2). Larger clusters would result in direct connection between the clusters. To study if flooding-heterogeneity interactions affected the abundances of the strategies we combined the scenarios described above in all possible combinations in the third experiment. Every scenario runs for 100 years.

Analysis

The relative abundances of avoiders, invaders, resisters and endurers in the whole grid were documented in time and averaged over runs.

5.3 Results

Variation of plant strategies along a heterogeneity gradient

All simulations with one flood per year show the highest abundances for invaders and lower numbers for respectively resisters, avoiders and endurers (Figure 5.3A). Under this flooding regime, the abundances of invaders and resisters decrease with decreasing heterogeneity, and the abundances of avoiders and endurers slightly increase with decreasing heterogeneity. The highest relative change in avoider, resister and endurer abundances is shown between heterogeneity of 100 and 200 sites.

The strategies are differently distributed over the flooded and non-flooded sites as shown in Figure 5.4A for the reference situation. Invaders and endurers are abundant primarily in the flooded sites compared to the non-flooded sites. On the other hand, avoiders and resisters are mostly abundant in the non-flooded sites. The abundance of endurers in not-flooded sites decreases in time, while their abundance in flooded sites increases. This is in contrast with the increasing abundance of avoiders in not-flooded sites. The other levels of heterogeneity have similar outcome (not shown).

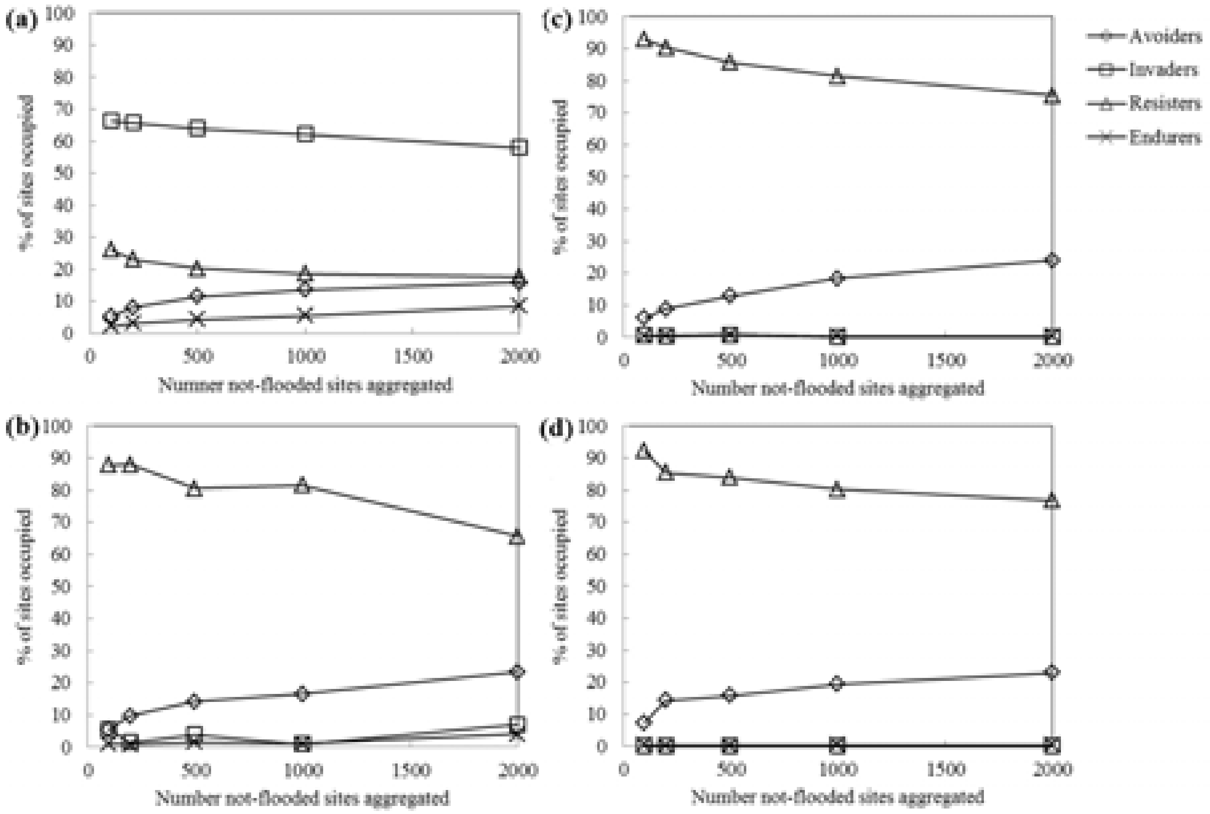


Figure 5.3. The relation between strategy abundances and heterogeneity for a scenario with (a) one flood per year, (b) one flood per 2 years, (c) one flood per 3 years and (d) one flood per 4 years. See Table 5.1 for strategy definitions.

The strategies are differently distributed over the flooded and non-flooded sites as shown in Figure 5.4A for the reference situation and Figure 5.4B with a flood frequency of 0.5. Scenarios with flooding frequencies of 0.25 and 0.33 show similar results and are therefore not shown. Like described before, the abundances of invaders and resisters strongly differs between the scenarios of one flood per year and one flood per 2 years (Figures 5.3, 5.4 and 5.5). Surprisingly, the relative abundance of resisters in flooded and non-flooded sites in Figure 5.4A opposes those in Figure 5.4B. The abundance of invaders and endurers in flooded and non-flooded sites is not distinctively different with less than one flood per year. With a flood frequency of 0.5, the abundances are characterized by variation, but stabilize after 50 years.

Variation of plant strategies with different flooding regimes

The flood regime affects the relative abundances of plant strategies (Figure 5.5A). The scenarios with a flood frequency of 0.25, 0.33 and 0.5 show the highest abundance for resisters, and lower abundances for avoiders, invaders and endurers. When the flood frequency increases from 0.25 to 0.5 the abundance of resisters slightly decreases and the abundance of invaders slightly increases. Simulating the frequency of 0.5 and one flood per year shows a big difference in the relative abundances of resisters and invaders. With one flood per year the invaders become the most abundant strategy instead of the resisters. And the resisters become second most abundant of all four strategies. The abundances of avoiders and endurers are similar in all scenarios.

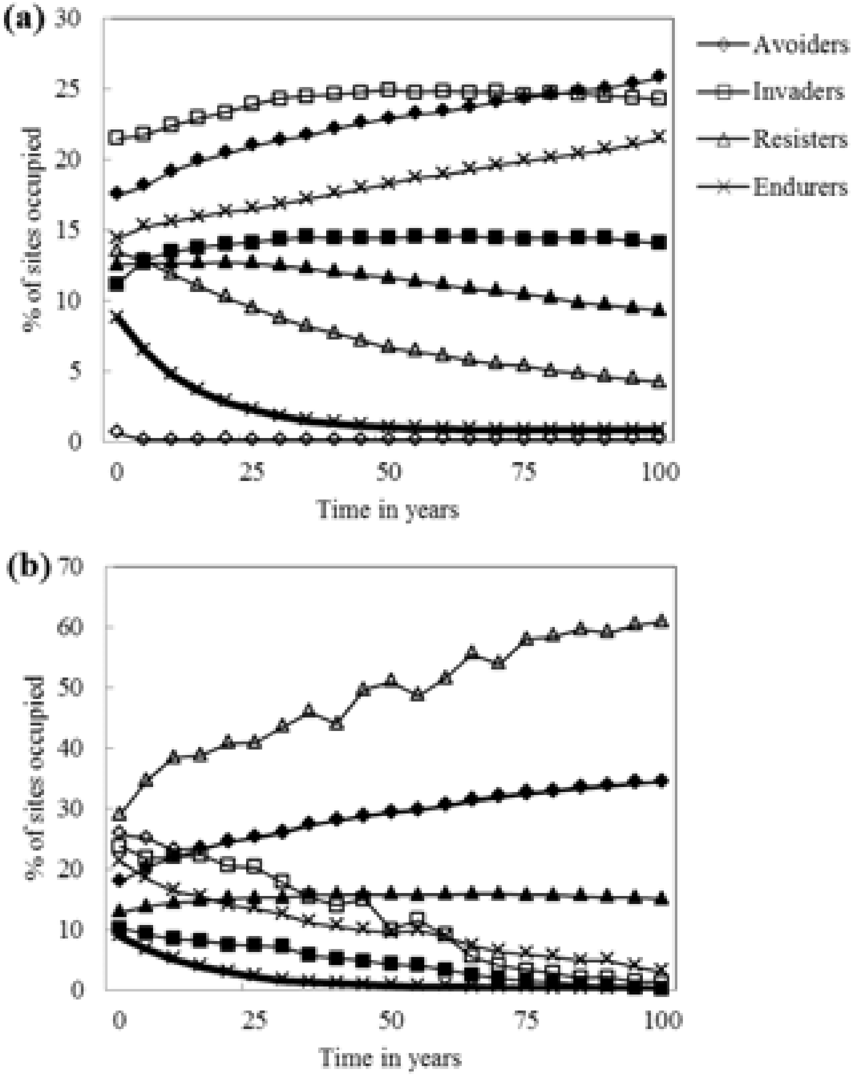


Figure 5.4. The strategy abundances in flooded sites (open symbols) and not-flooded sites (filled symbols) for a scenario with 2000 non-flooded sites aggregated and (a) one flood per year and, (b) one flood per 2 years. Note that in figure (a) both lines line of avoiders overlap, and the y-axes scales differ for (a) and (b). See Table 5.1 for strategy definitions.

Variation of plant strategies under interaction of flooding regime and heterogeneity

The scenarios with different flooding regimes and landscape heterogeneities combined show a clear effect of different flooding regimes (Figure 5.3). The scenario with one flood per year has the highest abundance of invaders (Figure 5.3A). Whereas the other scenario's with lower flood frequency show the highest abundance of resisters (Figure 5.3B, C and D). Avoiders and endurers are more abundant with one flooding per year compared to the other flooding regimes (Figure 5.3). The impact of changing flooding frequency on avoiders and endurers is however less pronounced.

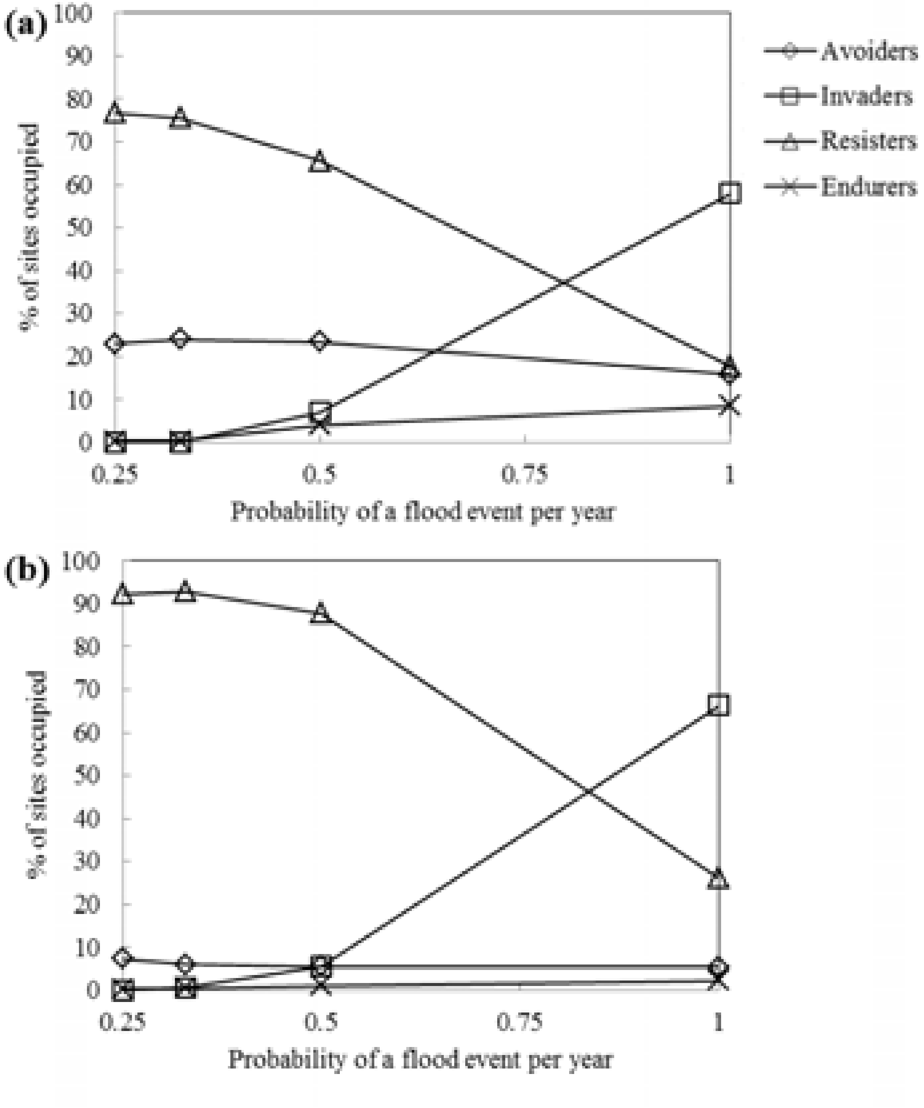


Figure 5.5. The relation between strategy abundances and flooding regime for a scenario with heterogeneity of (a) 2000 not-flooded sites aggregated, (b) 100 not-flooded sites aggregated. See Table 5.1 for strategy definitions.

A changing landscape heterogeneity also affects the strategies abundances (Figure 5.5). The results for heterogeneity of 100, 200, 500 or 1000 sites are similar and therefore we only show the results with 100 sites. The scenario with the lowest heterogeneity (aggregation of 2000 sites) shows the highest abundance of resisters (Figure 5.5A). Only with a flooding regime of once per year the invaders are more abundant. The scenario with the highest heterogeneity of 100 sites shows a similar pattern although the relative abundance of resisters is higher and the relative abundance of avoiders is lower (Figure 5.5B).

5.4 Discussion

The purpose of this study was twofold. First, to explore the variation of plant strategy abundances under changing flooding regime and along a landscape heterogeneity gradient, and second, to determine the effects of the interaction between flooding regime and landscape heterogeneity on the relative abundance of plant strategies. We found that the abundance of plant strategies changed with a changing flooding regime along a heterogeneity gradient. A decreasing heterogeneity resulted in a more even distribution of the strategy types. However, the effects of heterogeneity are small. With a decreasing flood frequency the relative abundances of invaders and resisters changed. With one flood per year the invaders were most abundant, but the avoiders, resisters and endurers also survived. When the flood frequency decreased only avoiders and resisters survived. Besides, with one flood per year the resisters' distribution over flooded and non-flooded sites was opposite from the scenario with one flood per 2 years.

The effect of changing heterogeneity on plant strategy abundances

We do not find strong effects of heterogeneity on plant strategy abundances. The absence of a relationship can indicate a strong ecological memory inhibiting ecosystem' responses to change (Peterson 2002). When the ecological memory is strong in ecosystems, landscape patterns are persistent. In our model the landscape configuration is fixed for every simulation. Such a stable landscape will select for an ideal strategy combination. To gain insight into the consequences of a stable landscape configuration we compared the strategy abundances in non-flooded and flooded sites. The invaders and endurers adapted to flooding ended up in the flooded sites and the avoiders, as a less adapted strategy, ended up in the non-flooded sites. An unexpected result of the heterogeneity simulations was that the resisters were modelled as well-adapted to flooding, but their response is similar to the avoiders' response. The results of this model suggest that a strategy like the resisters', with moderate parameter values, can survive in any landscape. Noticeable is the increase of avoiders' abundance with decreasing heterogeneity. Avoiders are perennial but have a very high sensitivity to flooding. Therefore they are most abundant in not-flooded sites from where they disperse high numbers of transient seeds. Such a strategy with a high external memory benefits from low heterogeneity. Because the chance to colonise a not-flooded is higher in homogeneous landscapes compared to heterogeneous landscapes Despite analogy with known demographic processes, the model omits dynamics that undoubtedly affect specific floodplain ecosystems. Further developments should include those processes more realistically. For example, incorporating a better representation of landscape heterogeneity to allow for more successional stages and to differentiate flood frequencies per site. Previous studies have shown the importance of spatial heterogeneity maintained by external drivers operating at different time scales (Ward and Tockner, 2001; Reich et al. 2003; Mathar et al. 2015). Connectivity supporting seed dispersal and affecting succession is also a critical factor to be incorporated (Cousins et al. 2003; Geilen et al. 2004; Corenblit et al. 2014).

The effect of changing flood regimes on plant strategy abundances

Changes in flooding regimes, involving altered frequency and magnitude of flooding, probably affect the floodplain habitats resulting in different vegetation diversity and dynamics (Capon and Dowe, 2007). Our study incorporated a reducing flood frequency, from one flooding per year to one per 2 years, per 3 years and per 4 years. The results show the largest effect when flood frequency changed from one flood per year to one flood per 2 years. With one flood per year the invaders were the most abundant strategy. Invaders are annuals and do not survive flooding, but due to their low adult longevity, invaders do require flooding to create open sites for germination. Of all strategies the invaders produce the highest number of persistent seeds to disperse over long distances (Bornette et al. 2008). So invaders have a strong internal and external memory. Endurers also show higher abundances with one flood per year compared to one flood per 2 years. Endurers are perennial and besides a low persistent seed production they have vegetative regeneration. Seeds and vegetative parts are dispersed over short distances. Thus endurers have a strong internal memory and need open gaps in the proximity to germinate (Bornette et al. 2008). With one flood per 2 years the most abundant strategy is the resister. Resisters are perennial and have a low sensitivity to flooding. As described before resisters survive in flooded and non-flooded sites. They produce not many persistent seeds but seeds are dispersed over long distances. Such a strategy has a diverse ecological memory. The survival as an adult can be seen as an internal memory, and seed dispersal as internal and external memory. Such diverse ecological memories favours resisters' survival under different environmental circumstances. The flood regime hardly affects avoider abundances. Avoiders lack a seedbank. Therefore avoiders are not able to win seed competition and to germinate in temporary undisturbed flooded sites. Our results correspond with the model simulations of highly regulated flow regimes resulting in variable cottonwood populations prone to local extinction (Lytle and Merritt, 2004). Their results show that frequent floods result in small but stable populations. This results from the trade-off between floods as mortality-causing vs. germination-enabling events. With frequent floods, germination occurs almost every year but strategies are supressed by flooding, resulting in low but stable abundances (Mathar et al. 2015). When floods are less frequent, adults survive over decades and are then suddenly flooded, resulting in varying abundances and extinction when return intervals of floods are long. The overall importance of seed production and dispersal show that ecological memory is generated in dynamic ecosystems dominated by external drivers like flooding (Peterson 2002; Bornette et al. 2008; Enright et al. 2014).

Effects of the interaction between landscape heterogeneity and flooding regime on plant strategy abundances

The interacting effects of landscape heterogeneity and flooding regime on plant strategy abundances does not differ from the separated effects. Avoiders are most abundant with low heterogeneity for all flood regimes. Invaders and endurers' abundances are almost independent of the heterogeneity and have the highest survival with one flood per year. Resisters are most abundant with high heterogeneity and less than one flood per year. Overall, our results suggest that heterogeneity with aggregated clusters of 2000 non-flooded sites will provide a suitable landscape for all strategies. However, invaders and endurers cannot survive when flood frequency drops below one flood per 2 years. So, our results underscore the importance of landscape heterogeneity and floods for the maintenance of floodplain ecosystems.

5.5 Conclusions

The model presented here identifies those strategies most vulnerable to variation in flooding regime along a heterogeneity gradient. The results show that the abundances of all strategies are preserved with heterogeneity of 2000 sites aggregated and one flood per year, whereas a higher heterogeneity or a lower flood frequency resulted in a loss of strategy types. These results illustrate that reorganization after a flood is dependent on the amount of internal and external memory (see Figure 5 in Bengtsson et al. 2003). The strategies relying on an internal memory profit from large aggregated clusters, whereas strategies that contribute to the external memory survive in any landscape. Our results confirm the suggestion that to maintain resilience in ecosystems managers need to incorporate disturbed areas and the surrounding landscape.

Chapter six

Synthesis, discussion and conclusion

6.1 Objectives and structure of the thesis

Environmental change threatens the ecosystems on which humanity relies, at different spatial and temporal scales. To support ecosystems, the conventional strategy of ecosystem managers and policy makers is trying to reduce external pressure and to control internal dynamics. However, ecological responses to human intervention can be surprising due to ecosystem complexity. Therefore, an increasing interest is emerging among managers and policymakers to enhance ecosystem resilience as a strategy to maintain ecosystem functioning. This approach relies upon the abilities to operationalize resilience. In the previous chapters I have investigated how species traits, environmental variability and landscape structure interact and how these interactions contribute to the ecological memory of an ecosystem. I used the knowledge gained to identify key mechanisms of resilience operating at the level of individual species, populations and communities. The following research questions were addressed:

1. How to link local environmental variability to species traits in order to assess an ecosystem's resilience to change?
2. Which interactions between spatial heterogeneity and traits affect resilience?
3. Can species traits be used to identify mechanisms underlying an ecosystem's ecological memory?
4. How does the interaction between environmental variability and landscape structure affect the adaptability and transformability of ecosystems?

In this final chapter, I synthesise the findings of the previous chapters and summarise the answers to these research questions. I also reflect on how the answers to the research questions relate to ecosystem management in the context of a rapidly changing world.

First, I elaborate on the use of a response-and-effect framework for plant traits to understand and assess ecosystem resilience at a local scale. Subsequently, I reflect on the different responses of plants and butterflies to the extent of spatial heterogeneity in wetlands using species traits related to resilience. Next, I address how management can enhance the adaptive capacity of an floodplain ecosystem by using plant traits as an indicator for ecological memory. Than,, I show with a spatial explicit, demographic model of a floodplain ecosystem how the interaction between disturbance regime and landscape heterogeneity affects the ecological memory. Finally, I discuss the relevance of the results for ecosystem management and reflect on the overall aim of this thesis.

6.2 Using response and effect traits to assess ecosystem resilience

In the study described in Chapter 2, I adapted Suding's effect-and-response framework (Suding et al. 2008) to understand how communities interact with the environment. I used response traits, associated with resistance to environmental variability and effect traits which influence species recovery (Diaz and Cabido 1997). I related environmental variability with response traits and response traits with effect traits to study the system's tendency to resilience. In such a framework, abiotic parameters influence the functional trait composition of the vegetation. The shifts in species composition and the extent to which plant species differ in their traits determine the change in resilience. Combining insights from individual species makes it possible to extrapolate to the community level (Suding et al. 2008). As a case study I used wetlands because they provide essential ecosystem services, such as water retention and purification, and they are very sensitive to environmental changes. My results show that combinations of traits that specify effects of environmental change on ecosystem resilience can be identified. Species trait composition showed a strong resistance to environmental variability and, consequently, a positive effect on resilience. Moreover, our framework revealed that abiotic factors such as nutrients load, moisture and pH were strong drivers of trait composition. This provides a potential key to managing for ecosystem resilience.

The use of species traits is a valuable method to compare species responses to environmental change and to generalize species effects on ecosystem functioning. Numerous empirical studies have made considerable progress in elucidating which plant traits are relevant to the distribution of species along gradients of nutrient availability, disturbance and climate (e.g., Diaz et al. 2004; Evju et al. 2014). Nevertheless, every ecosystem has its own specific environmental factors (e.g., landscape heterogeneity, community composition, physiology) interacting with environmental processes. Some of these pathways are well understood, but others are still unknown. At this local scale I demonstrated that a response-and-effect framework for ecosystem resilience can be a useful tool for ecosystem management to define goals focussing on adaptation in changing environments. A complementary approach requires to focus on plant traits that can together represent the responses and effects of communities across scales. A possible difficulty of scaling may arise from an emphasis in ecology on context specificity at the expense of general principles (McGill et al. 2006). In this way, I argue to further validate the response-and-effect framework with empirical tests to understand and assess ecosystem resilience.

6.3 Linking spatial heterogeneity to species traits of plants and butterflies

Human-dominated landscapes are characterized by a mosaic of natural areas and human land uses, developed across environmental gradients. Increased levels of land use extent and intensity have well established negative effects on ecological processes (Fahrig 2003; Foley et al. 2005; Rockstrom et al. 2009). Spatial heterogeneity can moderate some of the negative effects of land use in human-dominated landscapes (Tscharntke et al. 2005). Most research shows a positive effect of heterogeneity on, for instance, population stability (Oliver et al. 2010; Oliver et al. 2014), dispersal (Atauri and de Lucio 2001; Marini et al. 2010) and population survival (Piha et al. 2007; Kumar et al. 2009). To develop effective management measures to maintain ecosystem functioning ecologists need to improve our understanding of how communities respond to spatial heterogeneity. That different species, within the same community, respond differently to spatial heterogeneity because of their traits, is well known (Violle et al. 2011). To understand how this in turn affects ecosystem resilience, I tested, in Chapter 3, the role of heterogeneity in trait selection across different spatial scales. This study was conducted for butterflies and plants in wetland ecosystems. I selected two indices of heterogeneity: (1) the Shannon-Wiener Index, which accounts for relative abundance and the number of land cover types, and (2) the Contagion Index, to calculate the configuration of the land cover types. For both butterflies and plants relevant traits contributing to the adaptive capacity of the ecosystem, were selected *a priori* to capture species resistance to and recovery after disturbance. The results show that heterogeneity indices and their spatial extent affect trait composition for both species. Butterfly species trait composition was correlated to the total length of linear landscape elements (e.g., streams and hedgerows) present and the diversity of wetland types. Plant traits on the other hand, correlated to the aggregation and diversity of land cover. However, I found no indication that the extent at which heterogeneity affects trait composition differed between the two species groups.

So far, studies addressing both heterogeneity indices (i.e. indices of landscape composition and landscape configuration) are scarce (Pasher et al. 2013). Studies that have focused on landscape indices suggest that aspects of configurational heterogeneity, such as patch size and edge effects, impact on species richness (Holzschuh, Steffan- Dewenter and Tscharntke 2010) and functional diversity (Barbaro and Van Halder 2009). However, there are possible confounding effects in these studies, as heterogeneity indices were not explicitly tested for independence. To disentangle the effects of different heterogeneity aspects, I combined the RLQ and the fourth-corner methods for assessing trait responses (Dray et al. 2013). Both methods are based on the analysis of the fourth-corner matrix, which crosses traits and heterogeneity indices weighted by species abundances. However, they differ greatly in their outputs: RLQ is a multivariate technique that provides ordination scores to summarize the joint structure among the three tables, whereas the fourth-corner method mainly tests for individual trait–heterogeneity relationships (i.e. one trait and one heterogeneity index at a time). Approaches like the one I applied here opens up a new research direction: the study of spatially-based ecological functioning in wetlands and in other ecosystems. To my knowledge, this research field is growing in freshwater ecosystems (REF) but is still in its infancy in terrestrial ecosystems. I argue that, focussing on traits at the community level provides insights into ecosystem functioning at landscape level and a basis for effective ecosystem management (Öckinger et al. 2012; WallisDeVries, 2014). The approach adopted in this study yielded insights into the effects of spatial heterogeneity on trait composition for the species of interest, thereby highlighting the importance of considering the extent of spatial heterogeneity and the effect this may have on ecological resilience.

6.4 Plant trait composition as an indicator for ecological memory

The concept of ecological memory provides a perspective on how the adaptive capacity of ecosystems can be enhanced through management. It specifies how ecological processes in space and time assist in the reorganization of plant communities in response to disturbances. Ecological memory (EM) is the comprehensive assemblage of information encoded in remnant resources that can reflect the historical disturbance and current situation, and determine the future trajectory of the community or ecosystem. Because it includes remnant resources, such as plants and the soil seed bank, EM is likely to affect system development following disturbance. EM is composed of an internal and an external component. The external (spatial) component is considered to be sensitive to landscape configuration and composition, factors that can be partially changed through landscape management (Peterson 1998). Therefore, it is important to mechanistically understand the link between spatial landscape characteristics, EM and system responses to disturbances. A key issue is how ecological memory affects responses to change as a result of interactions across scales. By studying for real systems how past disturbances have shaped community composition, measured through plant traits, it is possible to identify mechanisms behind ecological memory and their relation to management measures. The advantage of using traits over species is that the results can be extrapolated to other ecosystems, since species with homologous traits are expected to respond similarly to environmental filters. In Chapter 4, I present a generalized linear mixed-effects model that links environmental variation in management and floodplain dynamics, within and between sites, to plant traits that are considered relevant for ecological memory. I focus on floodplain ecosystems and riparian plants in the river Meuse, the Netherlands. The results show how different mechanisms intervene in ecological memory. Grazing enhances recruitment opportunities, both for internal reorganization and for colonization between sites. Dense vegetation structure selects for species survival and species ability to disperse over long distances. Hydrodynamics interact with seed dispersal mechanisms and seed persistence. The variability in ecological mechanisms found at different spatial scales, represent a memory that enables ecosystems to adapt to changes in the environment. For ecosystem management to maintain and use as much of this memory as possible it should incorporate measures at various levels of scale. While it is often possible for a manager to intervene at the level of a site, managing to maintain ecological memory over larger spatial scales becomes increasingly more difficult. Managers will face constraints in jurisdiction over larger spatial scales, trade-offs with other land use types such as agriculture and other management goals such as flood prevention, and financial constraints on the amount of restoration measures. Therefore, only few management plans explicitly consider the spatio-temporal dynamics to which ecosystems are subjected. With the analysis of ecological memory in Chapter 4, I provide knowledge about how an ecosystem absorbs disturbances, reorganizes, and maintains its adaptive capacity across scales. Although this study concentrates on floodplain ecosystems, I acknowledge that understanding ecosystem resilience, factors outside the system being studied must be considered. The broadening of management from focusing mainly on a single habitat or species to examining ecosystem functioning, is a promising effort that represents a step in the right direction. More collaboration with other land-users, like farmers, water managers, and tourism organisers could encourage resilience-based ecosystem management.

6.5 Capturing the role of ecological memory in a model

To study these interactions, In Chapter 5, I developed a spatially explicit, demographic model for plants, with four plant strategies – avoiders, invaders, resisters and endurers - classified by their adaptation to inundation, as caused by river flooding. I used the model to identify those strategies most sensitive to degree of landscape heterogeneity and/or flooding regime. The results show that the internal memory contributes to reorganization in the large habitat patches. When landscape heterogeneity increases, i.e. more, but smaller habitat patches develop and the role of internal memory decreases. The plant strategies relying on internal memory mechanisms, such as a persistent seed bank, perform better in landscapes with large patches. Plant strategies that rely on mechanisms of external memory, such as long distance seed dispersal, are able to persist under all combinations of landscape heterogeneity and disturbance tested. The diversity of strategies increased with increasing disturbance frequency. The model illustrates that reorganization after a flood event is dependent on the relative amount of internal and external memory (Figure 6.1). I conclude that to maintain resilience in ecosystems subject to disturbances, site management requires to be embedded in a larger scale management strategy, such that the network of habitat patches can maintain ecological functioning, and diversity, at the landscape scale.

Plant traits are increasingly used as link between species and ecosystem processes. While the field has seen rapid progress during the last decade, most of the work focused on processes based on primary productivity, nutrient cycling and pollination through time as a measure of resilience (De Bello et al. 2010). The assessment of resilience as a result of interactions across scales and between ecosystems, has been based on trait-based approaches to a much lesser extent (Spears et al. 2015). Floodplains provide a useful model system to study determinants of plant strategy distribution patterns within dynamic ecosystems. Flooding affects community composition by controlling demographic processes like mortality and recruitment, affecting subsequent competitive species interactions.

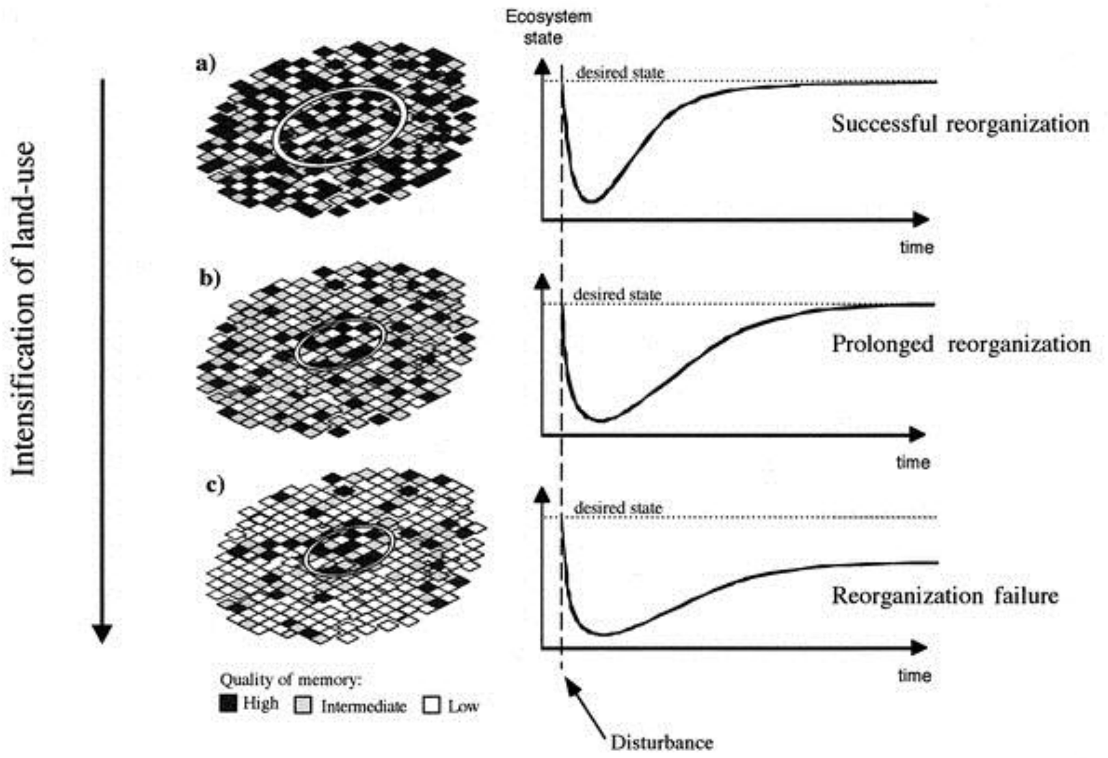


Figure 6.1. Reorganization of nature areas as dependent on the amount of internal and external memory. In (a), human land use is least intense, nature areas are large and rapid organization is achieved through a large internal memory. In (b), human land use is of medium intensity and the number of nature areas is smaller, but the smaller internal memory is compensated by the external memory in the surrounding landscape. In (c), human land use is dominant, nature areas are fragmented, and the diminshed external memory in the surrounding landscape is not sufficient to allow reorganization. From Bengtsson et al. (2003).

These community dynamics coincide with the hydrological gradient from river to the upland. As such, flooding acts as an environmental filter generating community assemblages with appropriate response traits. For the ecosystem to maintain resilience, ample arrival of strategies should take place across the hydrological gradient. Arrival of plant seeds or vegetative fragments is controlled by flood events subjected to environmental change. The combined effects of environmental and dispersal filters on the community composition applies not only to floodplains but also to many other (zonated) ecosystems where spatiotemporal disturbances exist, such as forests (Peterson et al. 1998) and wetlands (Ortmann-Ajkai et al. 2014).

Landscape models like presented in Chapter 5, have been used to explore the influence of disturbances on vegetation dynamics and look for emerging patterns over long time spans (e.g., hundreds of years, Baker 1989). These approaches usually address biotic interactions between plant functional types that represent different components of a community. Landscape models explicitly focus on processes such as natural and human disturbances, and dispersal. For this reason they include simplified representations of the demography and biotic interactions. These simplifications of vegetation dynamics are essential to represent landscapes where local processes are over-ridden by large-scale disturbances and where habitat suitability is expected to be constant. With the presented model, I was able to show why the concept of ecological memory is fundamental to understand ecological resilience in dynamic ecosystems. The inclusion of more model parameters would permit more realistic estimates of potential species responses to environmental change. For example, this could account for the interactive effects of landscape dynamics and environmental changes to account for idiosyncratic changes that may be occurring throughout different parts of a species' habitat (Keith et al. 2008). However, such an approach also has several drawbacks, like the risk of model over-complexity. Including more parameters leads to an exponential increase of model interactions. As a consequence the effects of interest may be hard to deduce, and the model becomes a 'black box'.

6.6 Perspectives for operationalizing resilience

Opinions and notions advocating resilience thinking (e.g., complexity theory) are not yet part of the design and management of ecosystems. Though, the different meanings and interpretations suggest that resilience is a boundary object (Star 1988); an entity shared by several different actors but perceived differently by each of them. Resilience as a broad term fosters inter- or even transdisciplinary science ('bridging concept'; Davoudi et al. 2012) by providing space for building consensus on aims and interests. In this vein I argue that resilient systems need the capacity to explore and exploit. If so, the resilience concept can link day-to-day ecosystem management measures to theory by elucidating practical, yet effective, types of management interventions. I think that further operationalizing resilience can help to develop a discourse embraced by policy makers and ecosystem managers. In Chapter 2-5, I discussed certain elements that can contribute to this development. In the following section, I suggest how resilience can be applied meaningfully, to maintain ecosystem functioning in a rapidly changing world.

6.7 Scaling from communities to ecosystems

For many years researchers have studied the relation between species diversity and stability. With time, ecologists have refined their understanding of ecosystem dynamics, concluding that different measures are at play. For example, the idea that eliminating one species from an ecosystem might lead to radical changes in the entire ecosystem led ecologists to consider the importance of functional redundancy: if one species goes extinct, others are able to perform the same ecological functions, limiting knock-on effects. Functional ecology is the branch of ecology that focuses on the roles or functions, that species play in the community or ecosystem in which they occur. In this approach, so called species traits are emphasized.

Species traits - morphological, anatomical, biochemical, physiological or phenological features of individuals or their component organs or tissues - are a key to understanding and predicting the adaptation of ecosystems to environmental change. In turn, our level of understanding of how environmental change steers ecological processes determines the effectiveness of ecosystem management measures. One way to assess effects of future environmental change on ecological processes, is to make inference based on patterns in the current environment, or those in paleoecological records. Surely, studying these relationships and patterns has yielded important insights. However, forecasting, and managing ecosystem change based on these patterns, ignores the fact that future changes are expected to deviate substantially from current or historic dynamics. An alternative approach is to identify the mechanistic basis of the links between ecosystem functioning and environmental changes by scaling processes using a response-and-effect framework (Chapter 2). Indeed, the results of that study contribute to our mechanistic understanding of ecosystem functioning. A limitation, however, is that the study focussed on the local scale only. In addition, to consider multi-scale interactions and their role in ecosystem resilience would be important.

6.8 Nothing will stay, except for change

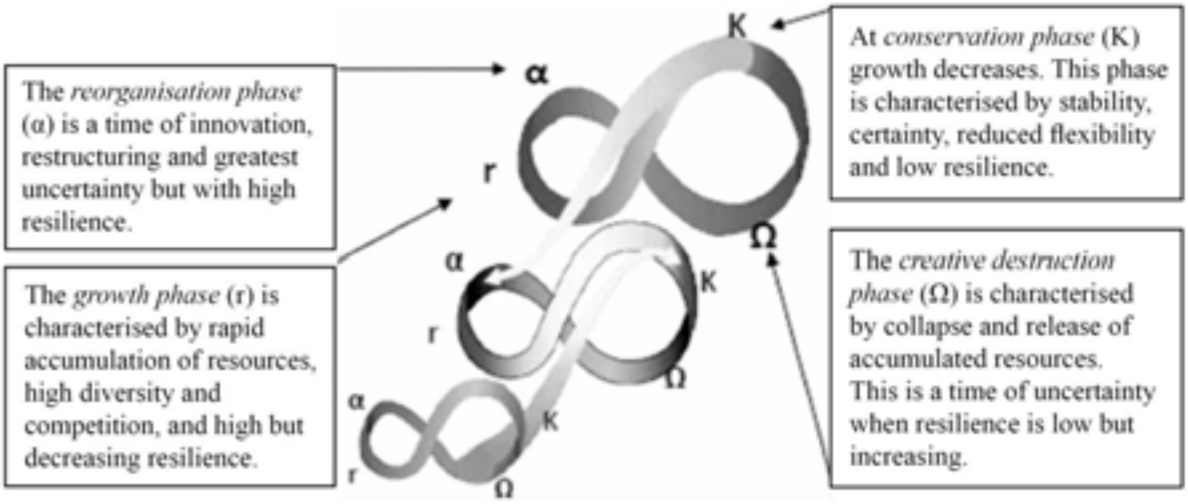
The shift from management focussing on species towards management focussing on processes offers new directions for management in the context of environmental change. A process-oriented approach favours a low-intervention philosophy: letting nature take its course but ensuring that the stage is effectively set for adaptation, especially in environments impacted by human activities. For ecosystems, this might include minimizing non-climatic stressors and conserving species diversity to optimize the availability of more species to maintain ecological functioning. For landscapes, this means including spatial heterogeneity (Chapter 3) and providing connectivity for species to shift and reassemble. The latter in particular has already entered the nature management policy agenda. But heterogeneity appears to be underused to date.

Ecologists increasingly acknowledge that if they want to understand the dynamics and patterns of ecosystems, they must go beyond studying internal system factors only and take external factors and inter-scale interactions into consideration. In Chapters 4 and 5, using the concept of ecological memory, I demonstrate the importance of incorporating different spatial scales to assess the impacts of environmental change on ecosystem resilience. By using a functional approach I detected the dominant processes that contribute to ecosystem resilience at different spatial scales. Panarchy, a term devised to describe the role of changes in dynamic ecosystems (Gunderson and Holling 2002) suggests that ecosystems are interlinked in continual adaptive cycles of growth, accumulation, restructuring and renewal. They do so at multiple spatial levels from plots, ecosystems and landscapes, at different rates from slow to fast and in various timeframes from short to long. Resilience in this perspective is not fixed but a changing process. Ecological memory broadens the concept of resilience to incorporate the dynamic interplay of ecological processes across multiple scales and timeframes (Bengtsson et al. 2003; Walker et al. 2004; Folke et al. 2010). I believe that internal and external memory need to be incorporated in ecosystem management, especially in human-dominated landscapes with altered disturbance regimes, such as flood regime and natural grazing. In practice, managers should recognize that disturbances are part of ecosystem development. Ecosystems can adapt to such disturbances if their size and heterogeneity match their dynamic responses to disturbances. In practice, this often requires management to take an integral landscape level focus including protected areas and production areas that together buffer the capacity to reorganize after a disturbance.

6.9 Future perspectives

In my view ecosystem resilience offers a useful framework, which inspires us to think in new ways about ecosystem management. These ways have a lot in common with adaptive management approaches and accepting ecosystem complexity including feedbacks and non-linearities. Adaptive management is an appropriate approach when the involved actors agree about the nature and extent of the problem, although it is uncertain whether the chosen measures will be effective because of uncertainty in understanding or unpredictability of the system response (Williams et al. 2007). Manipulating ecological processes always have uncertain outcomes because their time-space relationships are poorly understood (Cumming et al. 2013). Under these uncertain conditions, adaptive management provides a proper approach (Pouwels et al. 2011). As this thesis and other studies (e.g., Peterson 1998; Oliver et al. 2010; Enright et al. 2014) show, planning and management for ecosystem resilience entails numerous feedback loops and processes operating across spatio-temporal scales, and biotic and abiotic elements of the system. This complexity requires transdisciplinary research to interpret resilience as a multidimensional and theoretical concept to evolve adaptive management and policy making.

With time, the importance of spatial heterogeneity, functional redundancy and abiotic factors becomes clear. One of the next tasks that researchers need to accomplish is to develop tools to integrate the different aspects of resilience. I suggest to abandon the model with the ball on a multi-equilibria model (Figure 1.1) to represent resilience. Instead, I propose to use the panarchy model of adaptive cycles (Figure 6.2) to consolidate the different attempts to operationalize resilience for ecosystem management. This representation better visualizes factors and dimensions determining aspects of resilience mentioned in this thesis, in contrast to the multi-equilibria model.



The *reorganisation phase* (α) is a time of innovation, restructuring and greatest uncertainty but with high resilience.

The *growth phase* (r) is characterised by rapid accumulation of resources, high diversity and competition, and high but decreasing resilience.

At *conservation phase* (K) growth decreases. This phase is characterised by stability, certainty, reduced flexibility and low resilience.

The *creative destruction phase* (Ω) is characterised by collapse and release of accumulated resources. This is a time of uncertainty when resilience is low but increasing.

Figure 6.2. The panarchy model of adaptive cycle (adapted from Davoudi et al. 2013) .

To conclude, I imply that managing ecosystems in a rapidly changing world will largely be about facilitating nature’s response. To do this the right settings for abiotic and spatial conditions at local and landscape scales must be identified. Ecologists will need to learn to accept change but simulteanously use their capacity to influence outcomes through policy and on-the-ground action.

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Summary

Ecosystem management to date largely relies on command-and-control approaches using static target habitat types and species. The dynamic nature of ecosystems, enhanced by climate change and intensification of surrounding landscapes by a growing economy, makes such approaches increasingly ineffective. Ecosystem management and conservation policies are challenged to adopt approaches that build on dynamic views of ecosystems and changing environmental conditions as a central guiding principle towards more adaptive management and conservation strategies. The response of ecosystems to change is contained in the concept of ‘ecological resilience’. Resilience is discussed extensively in the scientific literature, but it needs to be operationalised for application in ecosystem management. In this thesis, I focussed specifically on adaptive capacity, i.e. the capacity of ecosystems to reorganize and maintain ecosystem functioning under changing environmental conditions.

From the ecosystem functioning perspective, the consensus that the loss of an individual species does not necessarily have obvious functional consequences, is growing. Rather, the species composition and the specific ecological roles captured by species traits within it, are central for ecosystem resilience. Following recent insights on the relationship between adaptive capacity and species trait diversity, I analyse how communities, through their trait diversity, respond to environmental conditions both locally and regionally. Plant trait databases are well developed and plant traits are extensively described in different contexts. In Chapter 2, I used response traits associated with resistance to environmental variability, and effect traits that influence plant species recovery, in an effect-and-response framework to study how such resilience mechanisms relate to environmental change. Species trait composition showed a strong resistance to environmental variability and, consequently, a positive effect on resilience.

Of the many factors that affect ecosystem resilience, spatial variation in environmental heterogeneity is commonly identified as one factor that is particularly relevant to managers. In Chapter 3, I tested how species trait selection related to landscape heterogeneity at different spatial extents. The analysis included butterfly and plant species characteristic for wetland ecosystems. Heterogeneity indices and their spatial extent indeed correlated with trait composition for both taxa, but I found no indication that the extent at which heterogeneity affects trait composition differed between the two species groups.

The concept of ecological memory provides a perspective on how the adaptive capacity of ecosystems can be enhanced through management. In Chapter 4, I use this concept to specify how ecological processes at different spatial scales assist in the reorganization of riparian plant communities after disturbances. The variation in ecological processes found suggests that internal and external memory can coexist, enabling ecosystems to adapt to changes in the environment. For ecosystem management to maximise this capacity of ecosystems to reorganise after disturbances, requires to incorporate measures at local, landscape and regional levels.

A central challenge in ecology is to understand the factors affecting ecosystem resilience across spatio-temporal scales. Such knowledge is needed as a basis for management measures and supports the translation of theory into practice. However, field studies are typically short in timespan and small in spatial extent. In Chapter 5, I developed a spatially explicit, demographic model with four plant strategies – avoiders, invaders, resisters and endurers - categorised by their adaptation to river flooding. I used the model to understand how flood regimes and landscape heterogeneity as a management measure to steer flood patterns, impact these different plant strategies. The model illustrates that community reorganization after a flood event is dependent on the relative amount of internal and external memory, which is in turn shaped by the degree of landscape heterogeneity.

I conclude that to maintain ecosystem resilience, site management needs to be embedded in a larger scale adaptive management strategy. In that way ecosystem management can effectively accommodate the dynamics of ecological processes. Guidance towards scale-inclusive management requires further operationalization of the concept of resilience. For this, the multitude and interplay of processes across spatio-temporal scales need to be assessed to understand which processes synergise and which dominate system responses. As the model of nested adaptive cycles indicates, to acknowledge that resilience encompasses multiscale interactions (across time and space), is important. However, to translate this crucial phenomenon in management measures is difficult. Resilience depends on many elements of complexity and perhaps the concept can never be perfectly captured. However, from its original descriptive meaning, resilience is becoming a ‘way of thinking’, a strong concept bridging disciplines, with the capacity to improve the effectiveness of environmental policy and practice – on the condition that the concept is made operational. With this thesis I contribute to this process by outlining and testing a number of dimensions along which resilience may be operationalized. Taken together, these dimensions offer various leads to research, policy and practice alike, to prepare ecosystem management for the challenges an increasingly dynamic world entails.

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Mens sana in corpore sano

(*Juvenalis*)

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Wageningen, 15 December 2015

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The SENSE Research School declares that **Ms Marjolein Sterk** has successfully fulfilled all requirements of the Educational PhD Programme of SENSE with a work load of 39 EC, including the following activities:

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