Is ecological succession predictable?

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Theory and applications

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ABSTRACT

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A literature study is presented on the predictability of ecological succession. Both equilibrium and nonequilibrium theories are discussed in relation to competition between, and co-existence of species. The consequences for conservation management are outlined and a research agenda is proposed focusing on a nonequilibrium view of ecosystem functioning. Applications are presented for freshwater-; marine-; dune- and forest ecosystems.

Keywords: conservation management; competition; species co-existence; disturbance; ecological succession; equilibrium; nonequilibrium

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Preface

Current policies and management guidelines on nature conservation are based on the idea of the balance of nature. Consequently, high predictability is assumed meaning that a desired quality and well-described natural state can be attained with suitable management. Precise targets are defined with respect to species and types of community that managers should preserve or recover in their reserves. Indeed, their funding is often based on meeting these targets.

The mainstream of scientific understanding on the functioning of ecosystem dynamics, however, is rather that ecosystems are in a state of nonequilibrium because of perpetual disturbances that occur at all scales. If so, the predictability of ecological succession may not be very high. In the context of climate change, meeting preset nature conservation targets may not be feasible.

In this literature study an overview is presented on equilibrium and nonequilibrium theories for the predictability of ecological succession. Examples and applications of the theory are presented for freshwater-; marine-; dune-; and forest-ecosystems. A research agenda is formulated with the vision in mind that nature conservation management should be based on a nonequilibrium approach.

Summary

The balance of nature or equilibrium paradigm consider that species living together in an area have a long history of joint evolution which caused that each species is adapted to a specific set of biotic and abiotic conditions, together representing its niche. It is thus assumed that the climate is stationary relative to the rate of adaptation. Although abiotic conditions form boundary conditions to which species must develop a life history so that it survives and reproduces in the first place, species differentiation is ultimately explained by biotic causes. Species differentiating resulted that competitive exclusion is effectively prevented leading to sustainable coexistence. Increasing specialization thus led to increasing species diversity. For example, discrete vegetation types can be discerned for a particular abiotic environment that are composed of co-evolved species and in that sense 'belong together'. This allows that incomplete or 'rump' vegetation types can be recognized in which species are missing but for which the empty niche is available. A species belonging to the vegetation type can thus easily invade the vegetation and claim its evolutionary assigned niche. Following disturbances, vegetation types are the unit of ecological succession as subsequent invasion of species take a predictable course. Population and community dynamics are thus assumed to be mainly controlled by density-dependent factors leading to numerical equilibrium between species. Research thus focuses on demographic behaviour of species which is why the equilibrium paradigm is also coined the demographic paradigm in ecology.

The nonequilibrium paradigm on the other hand, recognizes that nature is variable in space and in time at all scales and that stochastically occurring disturbances drive that variability. Hence, the adaptive response of species is ever lagging behind to changes in both the climate and biotic factors, effectively preventing co-evolution of species. Consequently, a vegetation is a loosely defined assemblage of plants rather than a closely knitted-together community so that discrete vegetation types indeed cannot be discerned. Co-existence between species, that share limiting resources, is then caused by the fact that competitive exclusion is slow relative to ongoing disturbances that newly make available these resources including nutrients, water and space. However, if disturbances do not occur for a prolonged period of time, competitive exclusion runs to its full extend and some species will become locally extinct. A species must therefore 'track' the availability of suitable sites to regenerate, establish, grow and reproduce for its sustainable existence. In the nonequilibrium paradigm, evolution shapes species with life history traits so that they uniquely respond to competitors; climatic factors; and the availability of regeneration sites created by disturbances, jointly determining the invasive capacity of a species. Ecological succession is then caused by the qualities of individual species rather than that of a community. The predictability of the course of events of succession is therefore low as it depends of the predictability of the disturbances. The nonequilibrium paradigm thus focuses on the individualistic behaviour of species, which is why this paradigm is also called the autecological paradigm.

The two ecological views, that either assume constancy and the balance of nature or that nature is inherently uncertain and unpredictable, may clash if applied to conservation management. It is conceivable that the probability of local extinction of some species increases if managed on constancy. Isolation and a 'command and control' approach of management for specific variables of interest can result in the erosion of resilience. This approach of management is valid if it can be assumed that the system operates near equilibrium and the control is sufficiently large so that deviations from equilibrium can be restored.

More natural ecosystems, on the other hand, are prone to inherently unpredictable events. Resilience, expressed as the system's ability to absorb those events, requires the occurrence of disturbances as otherwise the species that enable the renewal of the ecosystem in the first place, are lost. The management paradigm that considers surprises as inevitable and finds that knowledge is always incomplete, is that of adaptive management. Adaptive management aims at developing strategies that: 1) increases the buffering capacity of the system, by allowing small scale perturbations to operate to avoid large scale disturbances; 2) manages for processes at multiple scales; and 3) nurtures the sources of renewal.

Scientific concepts appear to have diverted indeed between equilibrium and nonequilibrium theory which has important consequences for conservation management. While a change in paradigm is a slow and confusing process in science, this is even more so if paradigms have been adopted in the political and societal arena. This appears to be the case for nature conservation and management.

Part I. Is ecological succession predictable? Consequences of equilibrium and nonequilibrium theory on ecological succession for conservation management.

Koen Kramer

1 Introduction

Current international policies for nature conservation such as the Treaty on Biodiversity of Rio de Janeiro, and the Birds and Habitats directives are based on a general idea of a balance of nature. Also in practical nature conservation management, aiming to meet the international agreements, high predictability is assumed that a desired successional stage can be attained after restoration of proper abiotic conditions and by taking the proper management. As a matter of fact, practical nature management is funded by governments depending on the degree that they attain the preconceived type that includes many threatened species. Scientific understanding, however, increasingly recognises that a perpetual state of nonequilibrium is characteristic of natural systems. This gap between policy- and management practise on the one hand, and scientific insight on the functioning of ecosystems and co-existence of species therein on the other, may prove currently applied conservation strategies to be invalid in fact not protect species and ecosystems they aim to conserve. Explaining what is being meant with the equilibrium idea on the balance of nature and what with nonequilibrium is the central aim of this review. It must be said that also within the scientific community no full agreement is attained on the importance of either equilibrium or nonequilibrium assumptions. A sketch of the issue is presented below, referenced in the main text, thereby introducing the structure of this essay.

Equilibrium theory on ecological succession assumes a transitive competitive hierarchy with a predictable asymmetric outcome based on life history traits. The predictability of succession and return to a previous successional state after a disturbance event depends on whether species are exchangeable and randomly mixed or that each species has its unique regeneration-niche. Classical theory on competition and coexistence states that for species to coexist they must differ in niche requirements. If species require the same resources at the same time, one species will outcompete the other in a stable environment based on a superior set of life history traits in the given environment. This theory thus supposes that the climate is stationary relative to the rate of evolution of species. Hence, the species have co-evolved leading to niche differentiation so that communities are comprised of species that "belong together". Vegetation types are therefore the unit of terrestrial succession, which is the basis of phyto-sociological classification. An

incomplete vegetation ("rump vegetation") is open for invasion by the missing species as the invaders niche is necessarily unoccupied. The equilibrium assumption for succession is that the pre-disturbed ecosystem is a stable state and that the successional pathway towards that state follows a predictable course of species replacement. It are the biotic interactions between species that determine the final stable state in terms of species composition and abundance. Any notion of history is lost once the stable state is attained. Nature conservation based on this view assumes that a desired successional stage, containing target species, can be attained after restoration of proper abiotic conditions and by taking the proper management measures.

The single stable state equilibrium theory is challenged by increasing theoretical evidence and empirical support that even with a gradual change of environmental factors, thresholds may be exceeded so that the ecosystem flips into an alternative stable state. Climate change may provide this environmental factor, but so are increasing fragmentation of the landscape, nitrogen deposition and many other human-induced changes. Important is to recognize that the predictability of both the trajectory and the final state of succession is uncertain in systems with alternate stable states. Conservation aims are, then, increasingly difficult to attain once the system is in an undesired alternate state.

Nonequilibrium theory on ecosystem succession is based on the idea that many ecosystems are in a state of nonequilibrium due to ongoing disturbances. Under nonequilibrium conditions competitive exclusion is effectively prevented by fluctuations in space and time of both the physical environment and of biotic processes. Local extinction is a common feature in a nonequilibrium environment as well as ongoing invasion from a local species pool. Both factors are caused by the stochastic nature of prevailing disturbances and species coexistence indeed depends on these disturbances. As the environment, including the climate, is variable at all scales the rate of adaptation is unable to track them. Hence, co-evolution between competing species has not taken place so that species form at best loosely recognizable assemblages of species but are not biotically controlled communities or discrete types in case of terrestrial vegetation. Under different environmental conditions in the past and in the future, the species composition and – abundance of an assemblage will therefore differ from currently recognized classifications. Species must thus dynamically track through dispersal and new establishment suitable environmental conditions to which they are adapted to fulfil their life cycle. Thus, species respond individually to environmental changes rather than as a closely knitted-together community. The predictability of ecological succession in term of species composition is much more unpredictable in the nonequilibrium view compared to the equilibrium one. Conservation targets in terms of species presence in a given ecosystem are much more difficult to attain, even more difficult in systems with multiple stable states.

It may be considered an academic question whether competitive exclusion is prevented either by niche differentiation or by ongoing disturbances. The absence of competition cannot be shown to operate in the field, whatever caused it. However, the right or wrong of either of these explanations for species co-existence and

diversity has large consequences for conservation management under environmental change. For example, take a previous species-rich meadow that lost many rare plant- and insect species due to nitrogen deposition and discontinuation of the annual moving regime. From an equilibrium point of view, it is the stable and consistent management that operated long enough to allow all relevant species to invade the system and fill their niches. The only option the manager has to bring the system back to the previous state is by re-instalment of previous nitrogen levels and previous management. This may be out of his or hers scope so that a loss must, regrettably, be accepted. The management focus will therefore be on protection of valuable natural reserves, rather than aiming to develop new ones.

From a nonequilibrium point of view, the species rich state was a situation far from equilibrium where competitive exclusion was prevented by the low growth rates relative to the repetitive disturbances caused by the mowing allowing perpetual invasion and establishment of new species. The increased rate of competitive exclusion due to the higher nitrogen levels can be compensated by installing a more intense disturbance regime. This –most likely- allows the species to find the set of conditions they are adapted to, though in different association with other species than previously. In the latter view, management should focus on defining and maintaining a new disturbance regime. Such a management may, however, have a tense relationship with the international treaties that stipulate the sustainable persistence of particular species in exactly defined types, which cannot be guaranteed. However, new and unexpected nature can develop, without sacrificing what already exists.

More specifically, the aims of this review are firstly, to provide an overview on predictability of ecosystem succession provided by equilibrium and nonequilibrium theories; secondly, to apply the theory for the management of aquatic and terrestrial ecosystems; and thirdly to formulate research questions for conservation management. This is done, with the explicit vision in mind that a nonequilibrium approach should be favoured for conservation management.

2 Ecological succession

2.1 Traditional view of succession

In the traditional view, succession is a pattern of changes in species composition of a community after a radical disturbance in the physical environment for colonisation by plants and animals. In a constant physical environment the changes in species composition slows down, resulting in a climax situation characterised by slow change in species composition (Horn 1974). Odum's definition of ecological succession was most explicit and influential for several decades of research (Odum 1969):

> "(i) It is an orderly process of community development that is reasonably directional and, therefore, predictable. (ii) It results from modification of the physical environment by the community; that is, succession is community-controlled even though the physical environment determines the pattern, the rate of change, and often sets limits as to how far development can go. (iii) It culminates in a stabilized ecosystem in which maximum biomass (...) and symbiotic function between organisms are maintained per unit of available energy flow. (...)"

These definitions suggest a clear pattern and high predictability. Nevertheless, authors felt it opportune to distinguish climatic-climax; pre-, and postclimax; potential climax; disturbance- of disclimax; ser-, eo-, and pan-climax; edaphic-, physiological- and topographic climax; pyroclimax; aquatic climax; biotic versus antropeic-, antropo- or archeological climax; para-, con-, ante- and peniclimax; trans-meta- and euclimax; deflected climax; plagioclimax; pseudo-, quasi and co-climax, pedoclimax, salt-spray climax and indeed superclimax (see references in (Whittaker 1953)) suggesting that towards what the successional trajectory is directing is not very much predictable indeed. Despite its vagueness and therefore suggestions to altogether abandon the term, Whittaker (1953) argues that for all its subjectivity and relativity the climax concept has real meaning and usefulness as an idealized state of constant species composition, whilst appreciating that species composition and their relative abundances fluctuate and varies between locations as the physical environment changes along more or less perceivable gradients.

Researchers of succession now largely agree that succession can only be understood as the statistical result of a species-by-species replacement process whereby complexes of species' traits, merged into adaptive strategies, determine the competitive outcome when individuals of different species encounter. This insight has profound consequences for the concept of a biological community in relation to ecological succession. Gleason (1926) is among the first to conclude that:

> "(...) every species of plant is a law unto itself, the distribution of which in space depends upon its individual peculiarities of migration and environmental requirements. Its disseminules migrate everywhere, and grow wherever they find favourable conditions. The species disappears from areas where the environment is no longer endurable. It grows in company with any other species of similar environmental requirements, irrespective of the normal associational affiliations. The behaviour of the plant offers in itself no reason at all for the segregation of definite communities. Plant

associations, the most conspicuous illustration of the space relation of plants, depend solely on the coincidence of environmental selection and migration over an area of recognizable extent and usually for a time of considerable duration. A rigid definition of the scope or extend of the association is impossible, and the logical classification of association into larger groups, or into successional series, has not yet been achieved."

Drury and Nisbet (1973) argue that we will not achieve that nor should aim for that higher-order classification to understand succession when they state:

"... the phenomena of succession can be understood as consequences of differential growth, differential survival (and perhaps differential colonizing ability) of species adapted to growth at different points on environmental gradients. The appearance of successive replacement of one 'community' or 'association' by another results in part from inter specific competition which permits one group of plants temporarily to suppress more slowly growing successors. The structural and functional changes associated with successional change result primarily from the known correlations in plants between size, longevity, and slow growth. A comprehensive theory of succession should be sought at the organismic or cellular level, and not in emergent properties of communities."

They find that a number of detailed studies of succession in forested regions do not conform to the contemporary generalization of Odum (1969) that observed phenomena are the action of the community itself in changing the environment. Nor did they find that later successional stages are necessarily directional, as structural and functional properties are generally inconsistently associated with species composition. Finally, they conclude that that effects of species already on the site appear frequently delay rather than facilitate successional replacement (Drury and Nisbet 1973). They observe that many successional patterns follow directly from the lack of empirical correlation between species that produce copious offspring which disperse over large distances and that are short-lived, and species which lavishly provision few offspring and that are long-living and thereby hoard limited resources (Horn 1974). Thus, Drury and Nisbet (1973) and Horn (1974) depart from the holistic community perspective proclaimed by Odum (1969) and state that ecological succession is predictable based on reductionistic principles. This view is now commonly accepted among ecologists and paved the way of explanations in plant succession towards underlying mechanisms based on physiological and genetic features (Bazzaz 1979; Bazzaz 1986).

2.2   Competition

Competition is one of the unsolved controversies in biology (Mayr 1997). This leads to ardent discussions in the literature between researchers with different views of both the importance, relative to other factors, and the severity, depending on circumstances, of competition. In succession theory the controversy is exhaustively analysed by the groups around Grime and Tilman. Although Grime's theory essentially focuses on the development of general plant strategies, it is discussed here as it provides a different view on competition and on ecological succession.
The equilibrium view of succession is that it is a series of competitive displacement of interacting individuals through utilization of a shared resource base. Differences in

utilization of the resource are then the result of differences in life history traits that individuals possess if they belong to different species. If species are too similar in life history traits one will outcompete the other. Thus to allow co-existence, a limiting similarity between species, i.e. a minimum niche divergence, is generally assumed (Abrams 1996; MacArthur and Levins 1967). The definition of competitive exclusion and its relation to minimum niche divergence of Whittaker (in (Pickett 1980)), is much rehearsed by students in plant ecology:

> "(1) If two species occupy the same niche in the same stable community, one will become extinct. (2) No two species observed in a stable community are direct competitors limited by the same resources; the species in niche in ways that reduce competition between them. (3) The community is a system of interacting, niche-differentiated populations that tend to complement one another, rather than directly competing, in their uses of the community's space, time, resources, and possible kinds of interactions."

In a loose sense, competition relates to the demand of one or more resources by different organisms to grow and that one gets more than the other. If this happens long enough the organism that gets most will replace the other, and obtain exclusive access rights. The mechanism according to Tilman (1980) is that during competition the stronger competitor reduces the resource concentration below a level at which the poorer competitor can survive. The species with that requires and can tolerate the lowest resource concentration for growth and reproduction, R^*, logically wins the competition. R^* is thus an equilibrium resource concentration, which is the point where resource supply and uptake rate balance and consequently plant growth and losses equate. The model is qualitatively equivalent to that of Berendse et al. (Berendse 1994; 1989; Huisman 1994) which is an extension of the ideas on competition of De Wit (1960) by explicitly taking a specific nutrient loss rate of the plant into account as feedback with resource concentration (Huisman 1994). A resource is then defined as any substance or energy that is required for growth and reproduction of an organism and whose amount in the environment is reduced through its utilization by the organism (Huston and DeAngelis 1994). An equilibrium assumption in resource competition theory is that resources and organisms are sufficiently mixed so that all organisms experience the same resource concentration and that the organisms themselves regulate the resource concentration in the shared environment (e.g. (Huisman 1994; Tilman and Lehman 1985)). Diffusion and turbulence are then assumed to be sufficiently high to homogenize the resource in the medium at least over the distance between neighbouring species. These equilibrium assumptions can be relaxed by taking an individual based approach where the resource utilization-, supply and transport rate of a resource in the vicinity of an organism are explicitly taken into account. In that situation the organism may affect its own resource base but not that of a neighbouring organism (Huston and DeAngelis 1994) so that competition is thereby effectively prevented by spatial heterogeneity. Although Tilman included spatial aspects in later version of his model (Tilman 1994) and analysed it with respect to transient behaviour, both nonequilibrium issues, the here on the equilibrium aspects of the resource ratio theory.

Thus, succession as described by the early version of the resource ratio theory is '... a shifting equilibrium where the dominant species at any point in time is the superior competitor for the particular conditions (ratios of resources) at that stage of succession.' (Grace 1991). As it are the interacting species that determine both the amount and the ratio of the resources, predictability of ecological succession is considered to be high and the role of stochastic factors is not relevant, at least in the purest form of the theory. However, later developments of the theory do include aspects of environmental heterogeneity and colonising capacity (Tilman 1994; Tilman 1996).

The theory of Grime (Grime 1977; 2001) is particularly concerned with the life histories and resource dynamics of established organisms to produce a functional classification of organisms for the analysis and management of communities and ecosystems. It was not designed to expose the vital roles of different kinds of juveniles in ecological processes, whose circumstances for establishments may be quite different from those of the parent. For that purpose, classification in regenerative types are needed that focus on dispersal, dormancy and parental investment which are included in a later version of the theory (Grime 2001). The rationale of the theory of Grime is that organisms face differences in intensity of disturbance rate, determining the period during which resources can be taken up, and differences in intensities of stress, determining the degree to which growth is hampered by biotic and abiotic factors. He argues that 3 major plant strategies have evolved which are syndromes of universally important traits for the functioning of any community or ecosystem. Under circumstances of low intensity of disturbance and low intensity of stress a set of traits evolved that enables the plant to be most competitive in productive habitats. The combination high disturbance and low stress favours a ruderal strategy, and the combination low disturbance and high stress favours a stress-tolerant strategy. The fourth logical combination, high intensity of disturbance and high intensity of stress allegedly has not viable strategy (Grime 1977). The competitor (C) strategy, is characterized by low reproductive effort and high growth rate; the ruderal (R) strategy by a high reproductive effort and high growth rates; and the stress-tolerating (S) strategy by both low reproductive effort and low growth rate. Also the later stages of succession are considered as biologically stressful conditions thereby favouring a stress-tolerating strategy. As an important element of these strategies is that of phenotypic plasticity, which is the degree to which an organism can functionally adjust itself if environmental circumstances change and which should have a genetic, i.e. evolutionary, base (Bradshaw 1965). S-strategists are considered to have low plasticity, its growth and reproductive rate is also slow in productive habitats, whilst a C-strategist can quickly adjust its morphology and/or ecophysiological functioning with increasing resource availability (Grime et al. 1991; Grime et al. 1986). As an example for plants, the high plasticity of the competitor strategy implies that it has a high uptake rate of both above ground *and* below ground resources by optimizing its allocation. The C-strategist is inevitably a good competitor for below- and above ground resources (Thompson 1987) because of the interactive nature of resource capture by leaves and roots: photosynthates are required for root growth and nitrogen assimilation in the roots and nutrients are required for the production of photosynthates (Grime 1994). It is

this aspect of optimisation versus that of trade-off of allocation pattern that the resource ratio theory clashes with that of the CSR theory. This positive correlation among its abilities to take up different resources (Grime) *vs.* a species will have a negative correlation among its abilities to tolerate and compete at low levels of different resources (Tilman) (Grace 1991) is falsifiable, but still appears an unsolved issue (Grime 2001).

Succession in the view of the CSR theory is caused by feedbacks between organisms and their environment, thereby changing the environmental sieve which differentially selects for organisms that either better tolerate the altered conditions or inhibits the occupancy of the site by other species (c.f. (Connell and Slatyer 1977)). The predictability of ecological succession in the CSR theory is thereby tightly linked to the predictability of environmental changes and stochastic factors play an important role in the rate of change of the sieve. The CSR theory thus adheres to a nonequilibrium explanation of species co-existence which is treated in more detail later in this essay.

Although Grime and Tilman support qualitatively the same definition of competition, that of differential utilization of shared limiting resources based on life history traits, Grime applies it to a narrow set of circumstances where the concept is applicable by excluding disturbance and stress as elements of competition, whilst Tilman uses a broad set of circumstances where it is applicable by including the disturbances and stress. Stress is effectively included in Tilmans concept of competition by dismissing stress as a useful ecological concept because different types of stress favour markedly different species and thereby different life history strategies (Tilman 1987b).

2.3   General patterns in succession: diversity, stability, productivity

At the community and ecosystem level, predictability of succession refers to recognizable patterns of stability, diversity and productivity. Horn (1974) reviews the traditionally view of ecological succession, essentially relevant for sessile organisms. However in later literature many of the claimed general patterns are contested. Therefore later sections describe deviations of the general pattern, for example in frequently disturbed and/or fragmented landscapes.

Predictability of recognizable patterns of succession is strongly linked with the concept of stability. Stability has in ecology, however, many interpretations and definitions. Stability defined as the absence of species turn-over tautologically increases with succession, as succession is defined as any development towards a climax which is a stage recognized by a low species turn-over. Stability defined as resistance to invasion also increases as succession proceeds because resistance, characterized as the successful abortion of invading species by means of the life history traits that enable a species to out compete other species, is indeed the mechanistic base of succession as formulated by (Drury and Nisbet 1973). Stability defined as resilience, expressed as return time to the original state after a disturbance, declines with successional development. This is because late successional stages tend to be composed of long-living species that consequently need a long time to recover, whereas early successional stages tend to be populated by sort-living species that thus

can quickly recover. Hence, a clear general pattern in stability of succession indeed exists. What is important for any quantitative definition of stability is that it continuously increases or decreases as succession proceeds. Some of such measures will be discussed in the sections on predictability of equilibrium and nonequilibrium succession.

Another stipulated pattern is that, when extensive and chronic disturbances are not prevalent, diversity of the climax is lower than that of some preceding stage. The reasoning is that a small disturbance, which does not change the relative proportions between prevailing climax species, allows either the invasion of a few additional species as pioneers, or the increase in abundance of early successional species that are already present, but rare. In both cases the diversity of the climax increases by a sufficiently small disturbance. Hence some stage of succession preceding the climax must exceed the diversity of the climax. This notion of climax thus corresponds to the stochastically blurred successional patchwork as accepted by Whittaker (Whittaker 1953). Diversity among climax species is then promoted by a number of factors, including: vertical stratification of air and soil, physical patchiness of the habitat, allelopathy, symbiosis, differential predation, diverse pollinators or dispersal agents, and exploitation of differential phenology (Terborgh 1973). This list indicates that other species are often the limiting factors for plant populations, so that diversity tends to be a self-augmenting process (Whittaker 1969). There is therefore no formal limit to diversity. However, in a continuous available and accessible environment, species tend to spread their distributions along gradients and sort themselves out until each location is equally saturated. Which should lead to a interpretable thus predictable pattern of diversity from place to place and from time to time (Horn 1974).

The third feature of succession that allegedly yields a clear general pattern is that of increasing productivity. Net primary productivity, expressed per unit area, is the net result of gross productivity and autotroph respiration. After a disturbance, gross productivity will exceed respiration because many resources, including non-productive free space, are made available. Net production increases as long as the production of new biomass exceeds respiration. However, with increasing non-photosynthetic biomass, increased shading and hoarding of nutrients in biomass, gross productivity declines and/or respiration increases. Hoarding of nutrients can even lead to a decline in productivity in late successional stages, resulting in total ecosystem biomass to reach some asymptotic value (Odum 1969). The predictability of this feature largely depends on the frequency and magnitude of disturbances and the response time of the ecosystem. Whereby the return time largely depends on available nutrients that either remain in the system; or that are released from the substrate; or that are input from elsewhere.

As stability, depending on the definition used, either continuously increases or decreases with succession and both diversity and productivity show a mid-successional hump, correlation between stability, diversity and productivity are typically positive for diversity and productivity, and are confounded for the other combinations. However, the mechanistic base for the interactions between diversity, stability and productivity is contested in the traditional and recent ecological literature. Some aspects of this controversy will be discussed below in the context of equilibrium and nonequilibrium theory.

3 Predictability of equilibrium succession

MacArthur and Wilson (1967) set a landmark in equilibrium thinking in that guided ecological research for many decades. Although they developed their theory for species diversity on islands of different sizes and distances from a mainland, the principle of an equilibrium between colonisation and local extinction had a profound impact on succession research (Whittaker 2000). The importance of island theory for ecological succession is, firstly, that it brought space and thereby the role of dispersal into the equation, which is at best addressed parenthetically in the traditional view. See e.g. the definition of Drury and Nisbet (1973) cited above. Secondly, it provided a exact assumptions and predictions to disagree with thereby allowing nonequilibrium thinkers to better formulate their ideas.

3.1 Neighbourhood stability

Stability is classically referred to as neighbourhood stability i.e. stability in the vicinity of an equilibrium in a deterministic system (May 1973a) essentially because that is mathematically most tractable. Given the central importance of the concept of stability for ecosystem predictability, the theory as presented in May (1973a) is outlined here.

If the rate of change in number or density of a population of a species is described by some function f:

$$\frac{dN}{dt} = f\left(N(t)\right) \qquad\qquad Eqn.1$$

The time-independent equilibrium is found by setting $f(N^*) = 0$ and solving for N^*. With N^* indicating the population size or density at equilibrium. Neighbourhood stability is then defined as:

$$N(t) = N^* + x(t) \qquad\qquad Eqn.2$$

With $x(t)$ a sufficiently small perturbation. To determine if N^* is stable or not, we need to find out of the system is inclined to return to N^* or to depart from it. This can be determined by using only the first, linear, term of a Taylor expansion around the equilibrium point. A 'sufficiently small perturbation' indeed means that all higher order, non-linear, terms of the Taylor expansion can be reliably ignored because that would make the analysis mathematically intractable. The first term of the Taylor expansion is:

$$\frac{dx}{dt} = ax(t) \qquad\qquad Eqn.3$$

with a the slope of f to N at the equilibrium point:

$$a = \left(\frac{df}{dN} \right)^*$$ *Eqn.4*

The solution for $x(t)$ is:

$$x(t) = x_0 e^{at}$$ *Eqn.5*

Thus, if the slope a around N^* is negative, it describes a valley and the disturbance dies away exponentially and the system moves towards N^*. If a is positive, it describes a peak and the system runs exponentially fast from N^*. If a exactly equals zero, it describes a flat horizontal line and the system is neutral. For example, for a single-species community with logistic growth it can be shown that $a = -r$, with r the net relative growth rate. Thus, fertility and mortality rates of a species, which determine a, are crucial features determining the rate of return to equilibrium after a perturbation (Pimm 1991).

Stability in a multi-species ecosystem is characterized by the interaction $a_{i,j}$ between species i and j:

$$a_{i,j} = \left(\frac{df_i}{dN_j} \right)^*$$ *Eqn.6*

Where $a_{i,j}$ are the elements of the community matrix **A** that describe the effect of species j on the rate of change of species i. Thus, $a_{i,j}$ can be seen as a measure of the resistance of a focal species to changes in density of other species in the community.

The solution for $x_i(t)$ is:

$$\lambda_j x_i(t) = \sum_{j=1}^{m} a_{i,j} x_j(t)$$ *Eqn.7*

The coefficients λ_j are called the eigenvalues of the system. Similarly as the analysis of a above, the sign of the eigenvalues determine the system's stability. The system is stable for all its components if all eigenvalues are negative, which most easily checked by determining the largest eigenvalue, *i.e.* the slowest responding species. However if any positive eigenvalue exists, then that component runs exponentially fast away from its equilibrium value. Eigenvalues can also have an imaginary part if, depending on functions f_i , a negative value emerges in a square root. In such a situation sinusoidal oscillations, or limit cycles, occur in the internal population dynamics *i.e.* in the absence of periodicity of external drivers. See May (1973a) for details of the interpretation of the real and imaginary part of eigenvalues for the pattern of stability.

A physical analogue of neighbourhood stability is that of a bowl filled with ping pong balls that is constantly wiggled around. Such a system is described as a potential pit plus random deviance. Although the stationary point is never reached as long as the bowl is wiggled around, it does lie in the centre of a probability cloud of balls that are constantly knocked around by the external force and many fold collisions. This picture then closely follows that of the blurred vision of the climax in the sense of Whittaker (1953).

Stability is thus a dynamic concept and is the consequence of opposing forces operating on objects: growth- and loss rates; fecundity– mortality; colonisation– extinction; gross productivity–respiration; incoming-outgoing nutrients; etc. Environmental drivers and feedbacks between these forces determine the position of hills, ridges, valleys, pits and wells along which trajectories of objects move. Note that the concept of *constancy* is related to the rate of change of an object itself. E.g., the number of ping pong balls in the bowl does not change if not shaken too violently. As constancy does not imply stability, it is crucial for the understanding of stability to differentiate between the vector field, possibly bowl-shaped, and the objects – individuals; populations; species; nutrients; etc. that move in it (Lewontin 1969).

Summarizing, neighbourhood stability is a yes or no test closely around a specific point. It does not indicate if an ecosystem returns to the original species composition after a large disturbance that moves the system far from equilibrium. Analysis of the size and shape of the basin of attraction around the stable point determines the resilience of the system. Based on the size of the basin of attraction predictions can be made how far the system can depart from equilibrium and still return to it. Whilst based on the shape of the basin of attraction, predictions can be made how fast the system returns to the stable point. If the pace of return is slow, new disturbances may occur before the system reaches the stable point and remains in a nonequilibrium state.

Furthermore, neighbourhood analysis yields no insight if the system is globally stable or that multiple stable states exist. The existence of multiple stable states is of particular importance for the predictability of the trajectory an ecosystem takes. If an ecosystem is pushed into the attraction zone of another stable point, it will not return to the pre-disturbance state but move to an entirely different species composition. Theory predicts that even a small disturbance or a gradual change of environmental driver can push the system over the separatrix that separates basins of attraction, if these exist. Resilience and the existence of multiple stable states are therefore essential features for the prediction of ecosystem succession and are discussed below.

3.2   Resilience

The concept of resilience that is used in the context of neighbourhood stability equates resilience with the time required to return to a stable state (Pimm 1991). The quicker the return time, the larger the resilience, the more predictable the system. As return towards the stable point goes at an exponential rate, a convenient comparative scale is if the magnitude of the perturbation decreases by the factor $1/e$, with e the

exponent of the natural logarithm. In that situation the interaction term between species, $a_{i,j}$ (Eqn. 5) equals $1/t$. The focus of interest is then the time interval at which the system moves the factor $1/e$ towards the stable point, *i.e.* what is the strength of the interaction between species? It can be shown that the length of the interval is the inverse of the largest negative eigenvalue (Neubert and Caswell 1997). Ecologically, the largest negative eigenvalues represents the lowest net relative growth rate found among the species composing the community. Indeed, the species that most slowly responds after a disturbance is the one that determines when the system attains equilibrium again. Return times have been determined for many forms of ecosystem complexity, including: species abundance, species diversity, food chain length, food web connectance and connectivity, herbivory and omnivory, energy flow, nutrient load and cycling, (see for references (Neubert and Caswell 1997; Pimm 1991)).

Resilience defined this way is an asymptotic property of the rate of decay of perturbations as time goes to infinity. However, a managers' main concern after a disturbance is the transient response of the system. Neubert and Caswell (Neubert and Caswell 1997) therefore propose a number of measures of transient responses to perturbations. The mathematical details are out of scope of the overview but their conclusion is that transient behaviour can be dramatic, long lasting and counterintuitive even in stable systems. They find that although a perturbation eventually decays, its size can grow rapidly at first and this growth can continue for times on the order of magnitude of the return time. That finding is true for linear systems and can be amplified by non-linear deterministic systems. Thus, without additional stochasticity, they conclude that an ecosystem can be highly unpredictable in its response to a perturbation. However, as with neighbourhood stability, this technique is only feasible when considering a sufficiently small perturbation so that only the first, linear, term of the Taylor expansion series needs to be considered. The mathematics becomes increasingly intractable or completely impossible for large disturbances where linearization around the stable point is not valid.

3.2.1 Multiple stable states

An important concept in connection to neighbourhood stability is that of *structural stability* of a *model*. The question is, does a small change in a parameter value result in a equilibrium value that is in the neighbourhood of the previous value, or does it result in a radically different equilibrium value? Put differently, do neighbourhoods of the parameter space map into neighbourhoods of equilibrium space (Lewontin 1969), or leads the trajectory to an entirely different stable state surrounded by its own basin of attraction? Structural instabilities, if they exist, make predictions very sensitive to model assumptions and make the development of a predictive theory of ecology a very difficult task indeed.

As an example, the classic deterministic Lotka-Volterra model of predator–prey interaction is structurally unstable because the equilibrium state of predators and preys switch between widely separated values if the intrinsic growth rate of the prey, *r,* exceeds a specific threshold. With even larger values of *r* this system behaves completely without any pattern or predictably, *i.e.* is chaotic (May 1976). Gradual changes in external conditions like nutrient deposition, climate change, habitat

fragmentation, harvest or loss of species diversity may cause a gradual change in ecological parameters and bring the system close to the threshold where a small perturbation may push it in another attractor zone resulting in large changes in ecosystem features (Scheffer et al. 2001; Scheffer and Carpenter 2003; Van Nes et al. 2004).

Scheffer (2001) provided a theoretical example and empirical support from lakes, coral reefs, woodlands, deserts and oceans that with a gradual change of environmental factors, thresholds may be exceeded so that the ecosystem flips into an alternative stable state. Looking at the state of the ecosystem while a control factor is slowly increasing, such as the nutrient loading or water level, a discontinuity can be observed. The ecosystem switches to an alternate state if a critical value of the respective control factor is exceeded. A subsequent decrease of the control factor leads to a switch back, but this occurs at a lower threshold value of the control factor than the forward switch, a process called hysteresis (see bottom projection of Figure 1). It is possible to bring the ecosystem back from one stable state to another by means of a disturbance provided that the control factor is within the range that allows alternative equilibria.
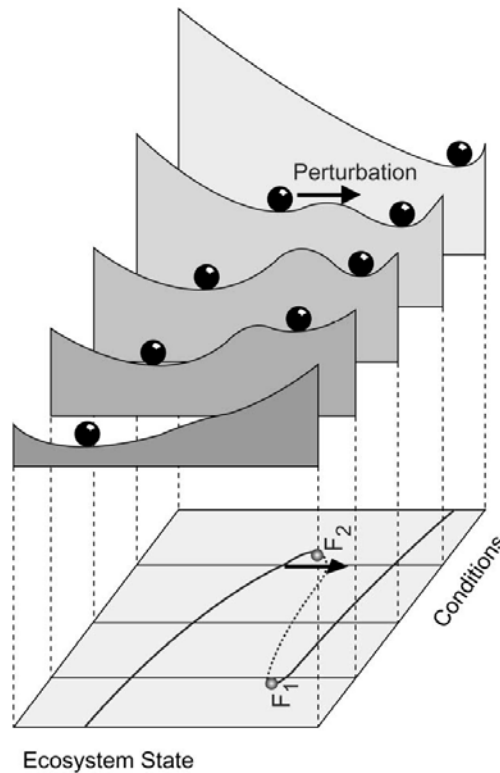
Figure 1: Clipped from (Scheffer et al. 2001). Accompanying text: "External conditions affect the resilience of multi-stable ecosystems to perturbations. The stability landscape depicts the equilibria and their basins of attraction at five different conditions. Stable equilibria correspond to valleys; the unstable middle section of the folded equilibrium curve corresponds to a hill. If the size of the attraction basin is small, resilience is small and even a moderate perturbation may bring the system into the alternative basin of attraction."

Van Nes et al. (2004) provide a full taxonomy of categorically different types of equilibrium dynamics. The general pattern is that multiple stable states exist as a result of positive feedback mechanisms and alternative, internally reinforced states, which can be caused by plant-soil (Adema et al. 2002, 2005), plant-plant (Wilson & Agnew 1992), or plant-herbivore interactions (Noy-Meir 1975, Van der Wal et al. 2000). For example, Rietkerk (1998) used the minimal model of Walker et al. (1981) to show that multiple stable states are the result of a 'humped' resource isocline in the resource–plant phase plane (see Figure 2a). Such a hump can for example result if at low plant density the infiltration rate of water is initially strongly reduced, but that this effect saturates at high plant density. Also for nutrients a hump is likely if at low plant density the nutrient loss is initially strongly reduced but that nutrient loss saturates at high plant density. Consequently, the resource isocline initially shows a positive slope, but with increasing plant density the losses due to water and nutrient consumption by the plants dominate, resulting in a negative slope. Hence the hump.

Herbivory increases the plant's minimal resource demand because resources are required for compensatory growth. Depending on the level of herbivory, 1, 2 or 3 equilibria exist between the resource- and the plant isoclines. If herbivore density exceeds a certain threshold (see Rietkerk 1988), a stable equilibrium exists at zero plant density; a stable at high plant density; and an unstable at intermediate plant density (Figure 2a). In that situation, even a small disturbance may push a system over the *separatrix* that divides the attractor basin of trajectories towards high plant density and that towards zero plant density. Successional trajectories in either of these attractor basins follow entirely different courses.
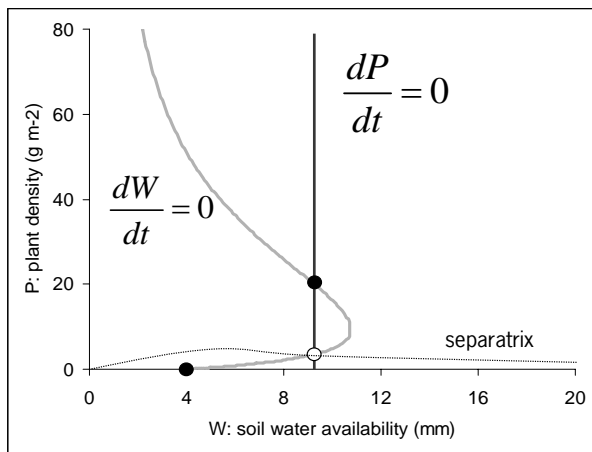

Figure 2A. Zero isoclines for soil water content (W, mm) and plant density (g m-2). 2 stable attractors (closed dots) are separated by an unstable point (open dot) (based on (Rietkerk and Van de Koppel 1997))
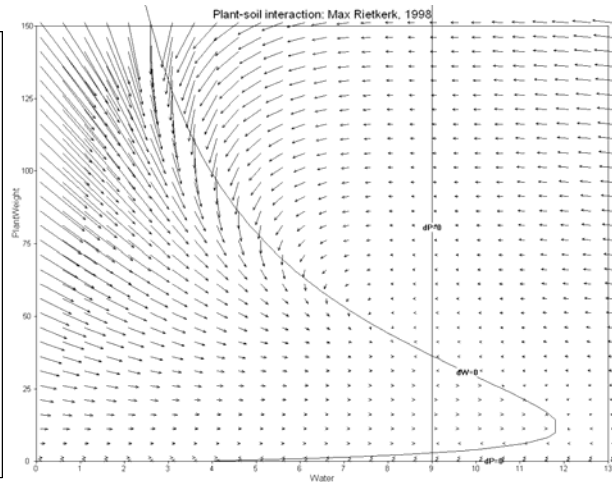
Figure 2B. Vector field for the plant – soil system of (Rietkerk and Van de Koppel 1997). The length of the vector is proportional to the rate of change.

Kramer et al. (2003a) found, using a complex mechanistic landscape model, that multiple stable states can be the result of the interactions between plant dynamics, herbivory and fire. In absence of fire and without regulation of the ungulate population (Fig. 3A), the system is highly dynamic with large seasonal changes in amplitude in both producer (total foliage) and consumer (total ungulate) biomass. Maintaining the ungulate population at low density and in absence of fire, reduces the ungulate biomass and make its dynamics more predictable (Fig 3B), whereas the seasonal changes in total foliage biomass and amplitude remain the same as in the previous situation. When including fire in the system where the ungulates are controlled at low density (Fig. 3C), periodically the system is moved towards a new stable state with reduced foliage biomass, i.e. grasslands instead of trees. However, return to the high foliage biomass is still feasible. When including fire in the system but with high ungulate density (Fig. 3D) this return to a forested state with high foliage biomass is not possible anymore because of ongoing high grazing pressure. Hence is this case the shift to another stable state is caused by a major disturbance, i.e. fire, rather than a gradually changing environmental factor, which is kept in that state by a continuously operating factor, herbivory.

The occurrence of fire is a stochastic process. Thus this type of shifts in stable states strongly depends on the probability of ignition. Varying the probability of ignition in this system, affects the build-up of fuel load and thereby the spatial extend of forest fires. The ignition probability furthermore determines the formation of vertical structure in the forest, in interaction with the herbivores, and thereby whether a ground fire develops into a crown fire (Kramer et al. 2003a).
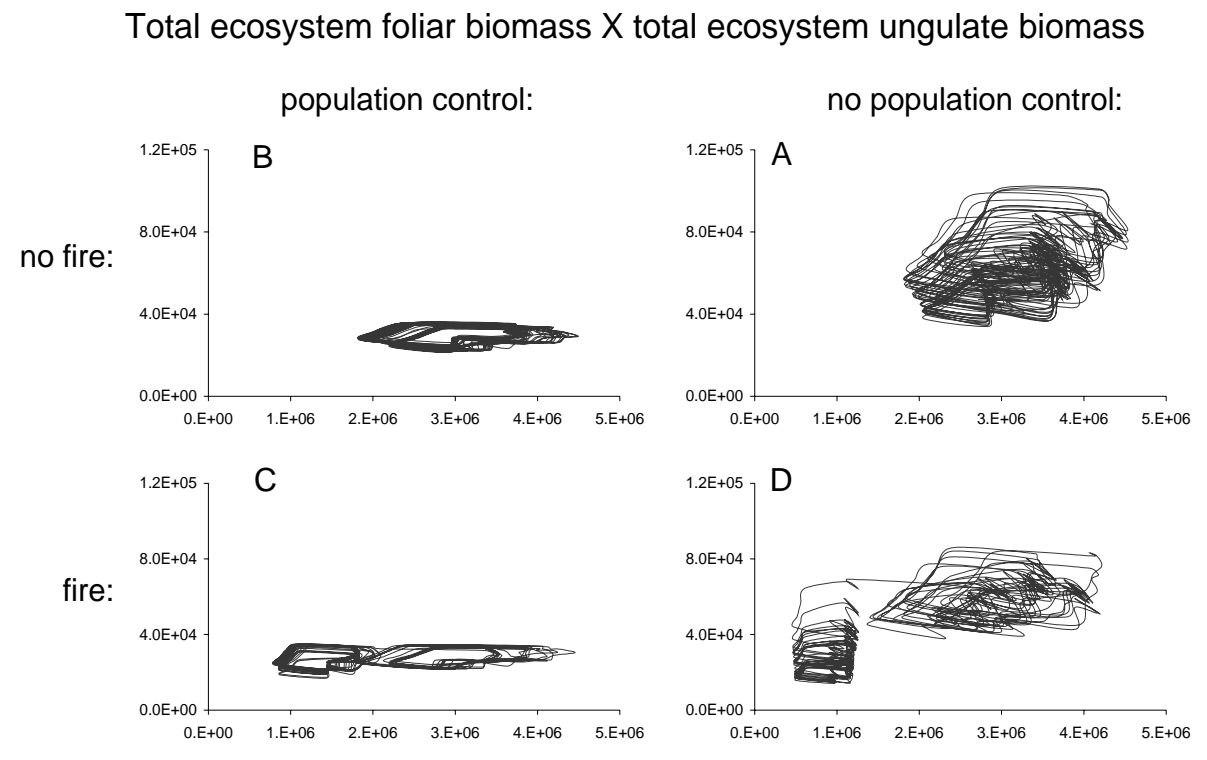
Figure 3. *Total foliage biomass of all plant species in herb, shrub and tree layer versus total ungulate biomass present in the Planken Wambuis area (phase diagram of producers vs. consumers), both without, and with, ungulate regulation and with or without the possible occurrence of forest fires (Kramer et al. 2003a).*

Succession is a process in which many species interact. Traditionally, it was argued and found that stability increases with species diversity, with one out of six arguments that model communities with only few species can be inherently unstable (Elton, 1958 in (May 1973b)). May (1972) effectively silenced the opinion that complexity begets stability with a few pages of matrix algebra by analysing the logical counterpart and concluded that multispecies model communities are never more stable than models of species-poor communities. The essential argument is that in multispecies communities the probability that some species interactions are unstable is larger than in species-poor communities, under the assumption that parameter values are assigned randomly. Depending in the strength of the interactions with other species, the probability that the whole system is unstable thus increases. (May 1973b). In a more recent analysis on randomly generated multispecies models, Van Nes and Scheffer (2004) found that multiple attractors may commonly arise from interactions between large numbers of species, especially if competition is

symmetrical and if interspecific competition is allowed to exceed intraspecific competition. Consequently, complex communities tend to move through occasional catastrophic shifts even in response to gradual environmental changes.

Summarizing, neighbourhood stability studies a system's dynamic behaviour after a sufficiently small perturbation around a point of attraction. Principally, only stochastic events that lead to small deviations from the stable state can be taken into account because otherwise the assumption to obtain the eigenvalues by taking a first-order, linear approach, is not valid. As the size of the basin of attraction is difficult to determine, resilience is best qualified as the return time to the stable state after disturbance. For large disturbances this must be done by explicit model simulation of trajectories. This can be an extensive task if many species are involved. For small disturbances the eigenvalues of the system provide sufficient analytical information and the most influential largest eigenvalue can be obtained, also for species rich models.

3.3   Temporal stability

Biologists and conservationists alike are often more interested in the constancy or variability, i.e. the temporal stability, of features of ecological characteristics instead of the concepts and consequences of neighbourhood stability. The concept of temporal stability is not restricted to equilibrium conditions but is in principle equally applicable to nonequilibrium conditions. It is discussed here under the equilibrium heading because the explanatory mechanisms of temporal stability are usually drawn from equilibrium thinking rather than from nonequilibrium theory.
Long lasting questions in ecology are then how constancy is related with species diversity (N) of an assemblage. The question in the context of this study is: Is a successional pathway that leads to a species-rich assemblage increasingly predictable, because more constant, or increasingly unpredictable, because less stable than assemblages with low diversity, as May asserts? Moreover, which impact do stochastic factors have on temporal stability?

Temporal stability is studied by Tilman (1999) elaborating on the statistical approach pioneered by Doak et al. (1998). Tilman's representation of temporal stability is outlined below without further repetition of this reference. Temporal stability (S) can be defined as the mean abundance (μ) standardized by its temporal standard deviation (σ): $S = \mu/\sigma$. The total community variance, and hence σ, depends on both the summed variances of the species and the summed covariances among all possible species combinations that compose the community. The covariance matrix thus represents the effects of interactions between species. It has a similar meaning in temporal stability as the community matrix **A** in neighbourhood stability (see above). Covariances are in most cases negative as the increase of one species is at the expense of another species, although indirect effects may result in positive covariances.
In the simplest case, species interactions are ignored so that abundances vary randomly and independently. Thus the community variance is the sum of the temporal variances of the species and covariances equal zero. To determine

community variance, the variance of species i may be scaled with its abundance, m_i, as a power function:

$$\sigma_i^2 = c \cdot m_i^z \qquad\qquad Eqn.8$$

With c a constant and z the scaling power. As the issue is was the increase or decrease of stability with increasing species richness, the relative community stability can be determined as ratio of stability with N species over the stability of a community composed of 1 species: S_N/S_1. Simplifying still further, let's assume that all species have equal abundances: $m_i = m / N$, with m total community abundance. For that case the relative community stability depends on species diversity and scaling power according to:

$$\frac{S_N}{S_1} = N^{(z-1)/2} \qquad\qquad Eqn.9$$

Thus, the factors that determine how variance scales with abundance critically determine temporal stability. If z equals unity, the variance of a species is independent of its abundance and the relative community stability independent of species diversity. The relative community stability declines with diversity if z is less than unity, and increases with diversity if z exceeds unity. In a number of studies including grassland and insect communities z was found to range between 1 and 2 (see (Tilman 1999) for references). This result thus indicates that temporal stability increases with species richness, N.

What now happens if community biomass changes with increasing species diversity? Does species abundance decline proportionally with species richness, less than proportional (overyield) or more than proportional (underyield) Thus, if species abundance scales with N:

$$m_i = \frac{m}{N^x} \qquad\qquad Eqn.10$$

then, for $x=1$ all species have equal abundances, for $x < 1$ all species overyield, and for $x > 1$ all species underyield. The community stability with species richness N relative to a community with 1 species can then be expressed as:

$$\frac{S_N}{S_1} = N^{1-x-(1-xz)/2} \qquad\qquad Eqn.11$$

Overyielding thus has a strong stabilizing effect. E.g. if $x = \frac{1}{2}$, relative community stability increases with diversity for all values of scaling power z, whilst underyielding has a destabilizing effect. E.g. if $x=2$, z should exceed 1.5 for stability to increase with diversity.

The above measure of temporal stability is at the community level. The same approach can be used to define the relative temporal population stability, by comparing the temporal stability of a species in a community of N species, $S_{1(N)}$, with that of its monoculture, $S_{1(1)}$. The relative population stability is, then:

$$\frac{S_{1(N)}}{S_{1(1)}} = N^{x(z/2-1)} \qquad\qquad Eqn.12$$

If z equals 2, population stability is independent of species diversity. If z is less than 2, population stability declines with species diversity, for all positive values of the overyielding coefficient x. Thus, the effect of overyielding is that it affects the magnitude of the impact of diversity on population stability but not to alter it qualitatively. Contrary to the effect of overyielding on community stability where low values of overyielding operated as a stabilizing force independent of the scaling power.

In general, given the empirical support that $1 < z < 2$, *communities* are likely to be more constant with increasing species diversity whereas *populations* are likely to be less constant. However, this conclusion is based a number of simplifying assumptions that are biologically unrealistic. Species do interact with each other thus covariances between species are not zero. Using a mechanistic model to determine these covariances, Tilman (1999) showed that the summed community covariance initially becomes more negative with increasing species diversity and less negative with higher values of N. The net effect of summed variances plus summed covariances is that indeed community temporal stability increases with diversity but population temporal stability slowly decreases. Succession leading towards a species-rich assemblage is thus likely to be more predictable in terms of community stability than species poor assemblages, even though population stability remains unpredictable.

The role of stochasticity in this general pattern is, firstly, that of temporal variability in abundance of a species due to variability in abiotic factors. This causes some species to decline in abundance thus giving other species the opportunities to increase in abundance. Variability of environmental drives are discussed in more detail in relation to population and community persistence (§ 3.3.1). Secondly, the role of stochasticity is that of the sampling of species that compose a community from a larger pool of potentially viable species. In the simplest case sampling is random, so independent of life history traits. So that half of the species underyield and half overyield. Thus with increasing sampling size, i.e. diversity, the probability that the most competitive species is present in the sample increases. Consequently, community variance declines proportionally to species diversity and stability, expressed as μ/σ of community biomass, increases proportionally with diversity because more diverse communities are, on average, more similar to each other than species poor communities at the same level of diversity (Tilman 1999). Although μ/σ of community biomass has a different interpretation as μ/σ based on time series of observations, both measures of stability show the general pattern of increasing community stability with increasing diversity. A logical consequence of the sampling effect is that a single species community that is perchance composed of the most

productive species can be as or even more productive as a highly diverse community that includes the most productive species as well as less productive species.

Though instructive, spatial and temporal heterogeneity in actual habitats make that the sampling effect has low biological realism as exclusive explanatory mechanism of stability. Niche differentiation between species make that they differ in their response to environmental factors. Hence, differ in optimal values and each species will cover only part of the habitat, but cannot exploit the entire range of conditions. In this model all species overyield. With increasing number of species, each with different optima, eventually the habitat is eventually fully exploited. Thus the total community biomass increases with diversity, consistent with the sampling model. Interestingly, with increasing habitat heterogeneity greater diversity is required to produce a given level of community productivity or coverage. As habitat heterogeneity increases with habitat size, larger habitats require greater diversity to attain a given level of productivity (Tilman 1999; Tilman et al. 1997).

The difference of this niche differentiation model and the sampling model is that community variance does not decline with diversity. At low diversity, habitat coverage is incomplete hence community biomass is less than in a community with even 1 additional species. Thus, habitat coverage increases by definition with more species rich assemblages. In the sampling model by chance the most productive species could have been sampled but also the most unproductive, producing a large variance around the average at low diversity. Here the role of environmental stochasticity and that of stochasticity in species sampling meet, as the degree of habitat heterogeneity is partly caused by stochasticity in abiotic factors, thereby providing the context how many species are required before full habitat coverage is obtained.

3.4   Features related to stability: persistence and resistance

Pimm (1991) defines *persistence* as how long a variable lasts before it is changes to a new value. Systems with low persistence have a high turnover rate. Persistence can thus be measured as the reciprocal of turnover rate and is expressed as time. *Resistance* measures the consequences when a variable is permanently changed for other variables of the system (Pimm 1991). E.g. if the consequence of changes in an abiotic driver on population density is small, the system has high resistance. Resistance of a variable can be expressed as the ratio of a variable before and after the change, hence is dimensionless. To compare persistence and resistance of ecosystems to environmental changes, it is crucial to be clear of what is meant with the 'variable' under study which in practise easily leads to confusion. For example, ecologists do their research on broadly 3 levels of organisation: population, community and ecosystem; analyse the results of 3 levels of complexity: species abundance, species composition and foodweb connectance; and use 5 concepts of stability: neighbourhood stability, variability or temporal stability, resilience, persistence and resistance. Hence, on average in 2.22% of the cases ecologist agree on the concepts under discussion. Although already statistically insignificant, its is a benign estimate of semantic agreement among biologists as (Nes et al. 2004) found no less than 163 definitions of 70 different stability concepts in the literature.

Note that also the concepts of persistence and resistance are not restricted to equilibrium conditions but also applicable to nonequilibrium conditions, as is temporal stability. However, in the literature it is usually used in the context of equilibrium theory and therefore discussed here in the equilibrium section.

3.4.1 Functional relationships between neighbourhood and temporal stability, resilience, persistence, and resistance

As stated before, a central question in succession research from an equilibrium point of view is: which factors determine how fast a population returns to the stable state after a disturbance? Pimm (1991) argues as follows. Firstly, if a population is below equilibrium density its reproductive rate is a major determinant of the return time, hence its resilience. If the population is above equilibrium density it is the mortality rate that determines resilience. Longevity, body size and storage, amongst other factors, will be important determinants of mortality. The processes governing 'down-resilience' are thus not the same as those determining 'up-resilience'. Secondly, resilience of a focal population also depends on species it is interacting with. If after the disturbance predators, also represented by herbivores, are removed, the return time to equilibrium will be much quicker than in presence of predators. The same holds true for the presence or absence of competitors. From the point of view of the predator however, the recovery of prey after the disturbance will be the main determinant of its return time. Thirdly, resilience will depend on how many resources are made available by the disturbance. If the disturbance removed most or all nutrient resources, the supply will depend on the mineralization rate and inputs from outside the system, making resilience much lower than if, besides fresh open space, large amounts of resource were made available by the disturbance. In summary, resilience is determined not only by life history traits of the species, but also on community- and ecosystem characteristics. Pimm (1991) provides many examples of research on each of these aspects.

The functional relationships between the different terms related to stability include that the life history traits which determine resilience, also affect temporal stability of populations and communities. A highly fecund species will quickly recover after a disturbance if resources are in ample supply and thereby show less variability in time than a less fecund species. Technically speaking, the less fecund species has the larger eigenvalue and determine the return time of the community (see Eqn. 7 and subsequent discussion). As body size and longevity are correlated with low fecundity, large and long-living species are likely to show low up-resilience and thereby larger variability (May 1973b). This contrary to the general observation that large species have lower temporal stability. Explanations that more resilient populations have higher rather than lower variability are, firstly, if there are time lags in reproduction and mortality. The recovering population then overcompensates by first overshooting and subsequently undershooting equilibrium density. Hence increasing its variability of the highly fecund species. Secondly, the equilibrium density may itself be stochastically variable, e.g. available space, suitable regeneration sites, nesting sites etc. The highly-resilient, highly-fecund species will be able to track that variability but the lowly-resilient, lowly-fecund species undercompensates and will

thereby show more temporal stability. If, however, growth rates are stochastically variable e.g. via supply of limiting nutrients, fluctuations are much higher than previously. And this is also most pronounced for the highly fecund species. Empirical evidence for mechanisms relating high resilience to either high or low variability can be found in (Pimm 1991). As forerunner to the nonequilibrium discussion, it can be concluded that the duration and frequency of the disturbance, relative to the reproductive rate of a species determine its variability.

Also species traits that determine its resistance affect the temporal stability of a species. For example, storage organs that are characteristically more associated with large, long-living species enable them to sustain more harsh environmental conditions. Thereby showing less variability than small, short living species that have fewer opportunities to survive adverse periods based on previously stored resources.

The ecological variables that are usually associated with persistence include that of either the density of a species at a location or the diversity of species in a community. The question is then: How long does is take before the species becomes locally extinct? Or: How long will a community maintain its species composition? The first issue is lies in the realm of metapopulation biology (Hanski 1997), whilst the second in (island) biogeography (Hubbell 2001; MacArthur and Wilson 1967).

An important issue relating persistence to understanding ecological succession is that of stochastic variability of environmental factors. The magnitude of environmental variation is widely acknowledged to be a crucial determinant of dynamics, especially of small populations. If all frequencies of variation in the environmental spectrum are equally important, this variation is referred to as white noise. Just as in while light where all wavelengths have equal weight. In that situation there is no correlation between successive environmental states and the noise is random. However, it is increasingly recognized that environmental fluctuations are temporally correlated and that this feature is likely to be critical in the growth and decline of populations (Pike et al. 2004). This means that infrequent environmental states have a disproportional greater influence on populations than frequent states. Hence, low frequent states are more important and the environmental noise spectrum is biased to long wavelengths, thus is reddened. The general finding is that if increased temporal autocorrelation in environmental variation affects the equilibrium density, K, extinction risk decreases, whilst if it affects growth rate, r, extinction risk increases. These results are highly dependent on the magnitude of the noise (see (Pike et al. 2004) for references) and are consistent with the findings presented above in the context of resilience and temporal stability (Pike et al. 2004), with the addition that more variable populations are more likely to get extinct, thus are less persistent. Moreover, if population dynamics are overcompensatory, increased environmental autocorrelation increases persistence, whereas autocorrelation reduces persistence in populations with undercompensatory dynamics (for references see (Pike et al. 2004)).

Reddening of the environmental noise and the importance of magnitude for dynamics and survival of populations and communities is rather abstract statistical phrasing for the fact that occasional large disturbances affect populations and communities more than frequent small deviations in environmental drivers. The theory is mainly mathematical, but it shows that strict analytical thinking takes a course from equilibrium towards nonequilibrium issues, which is the subject of the next section.

4 Predictability of nonequilibrium succession

There is no clear line of demarcation between equilibrium theory and nonequilibrium theory. In fact, nonequilibrium theory includes equilibrium concepts but extends the theory to arenas where equilibrium tools are longer not valid. This extension includes essentially 2 aspects.

Firstly, that of species co-existence and its consequence for diversity. Equilibrium theory applied to succession is based on the principle of competitive exclusion of species. Hence, species co-existence is based on concepts of limiting similarity (MacArthur and Levins 1967) and niche overlap (May 1973a). Disturbances may, however, cause that competitive mechanisms are not operational at least for some time so that the transient behaviour is of relevance and species diversity is the consequence of recurrent disturbances (Huston 1979).

Secondly, nonequilibrium theory explicitly addresses space over a range of scales, whereas equilibrium theory is valid on a specific scale only (DeAngelis and Waterhouse 1987). For example, the concept of carrying capacity is neither valid at a scale too small to contain a population, nor at a scale too large to also contain a large fraction of non-habitat. Nonequilibrium theory recognises that extinction of species is a common process at the local patch scale, whereas exchange between patches determines species persistence.

In the following, first general theories that aim to explain co-existence of species are discussed, followed by a more extensive discussion on disturbances that operate at a hierarchy of scales. These disturbances act as explanation for stability, diversity, and productivity in nonequilibrium theory.

4.1 Co-existence

Population models that aim to explain co-existence of species can be categorised in 4 groups based on the criteria of being open or closed to migration and assuming equilibrium or nonequilibrium dynamics (Caswell 1978). Closed systems are those where the population exists in a homogeneous habitat which does not receive or loose individuals or propagules from outside. Such migration is described in open models. The most important structural difference between those models is that zero is an absorbing state in a closed model but not in a model that is open to migration. Furthermore, spatial heterogeneity can be included in open models and this is not possible in closed model. As for the second ordering axis, equilibrium models focus on the properties of the system around equilibrium. Any notion of time is lost once equilibrium is attained. There are no inherent temporal dynamics anymore and the history of the system can not be retrieved once the system is in equilibrium. Nonequilibrium models on the other hand are essentially concerned with the transient behaviour of the system away from equilibrium and temporal dynamics are the main focus of attention. Combining both classifying schemes, four general types of models emerge: closed- equilibrium; open-equilibrium; closed-equilibrium and open-nonequilibrium (Caswell 1978). In succession theory, the early version of the

resource-model of Tilman can be considered a closed-equilibrium model. Later extensions include colonising ability and spatial heterogeneity and are thus open-nonequilibrium models. On the other hand, the CSR model of Grime can be categorized among the closed nonequilibrium models. Both models are discussed below with respect to the co-existence of species.

4.1.1   Resource-ratio theory

To explain the co-existence of many species on a limited number of limiting resources, the essence of Tilmans theory is that an organism needs more than one resource and that high efficiency in the utilization of one resource must necessarily be at the expense of the efficiency in the utilization of the other resource. Thus if there are only 2 resources, species are ranked in competitive ability for one resource in reverse order of their competitive ability for the second resource (Tilman 1987b). As an example for plants, below ground allocation of photosynthates for the uptake of nutrients or water occurs at the expense of above ground allocation to stems or foliage for intercepting and competing for light. For plankton a similar reasoning holds true (Tilman 1977). Co-existence is then the consequence of the differences between species in trade-off investments to take up different resources. Hence, it is the *ratio* of resource concentrations in the environment that enables species, that have evolved different life history characteristics, to co-exist (Tilman and Lehman 1985). In practice an unlimited amount of species are able to co-exist on shared limiting resources if they all differ in the ratio in which they minimally require and tolerate resources. Put in another way, an important prediction by the model is that evolution leading to high utilization efficiency of one resource, e.g. nitrogen, leads to different set of life history traits than for another resource, e.g. light. Furthermore, the resource ratio model always considers competition as the process that determines the displacement of one species by another during the entire succession phase. Although transient periods may exist before competition operates to its full extent. Other processes such as disturbances or herbivory are essentially included in this broad notion of competition through increasing the equilibrium resource concentration as additional resources are required to compensate for the loss of tissue. Hence, competition is considered to be equally important in nutrient poor habitats as it is in nutrient rich habitats. Changes in supply rates of nutrients and light must therefore be sufficiently slow, so that competitive interactions approach equilibrium at all times during the successional process (Tilman 1987a; Tilman 1987b; Tilman and Lehman 1985).

4.1.2   CSR theory

The theory of the competitor-, stress-tolerator- and ruderal- strategies to explain vegetation processes and ecosystem properties of Grime (2001) is an example of a – mainly- closed, nonequilibrium model for vegetation succession. Co-existence of organisms is in the CSR theory is essentially explained by variation in the environment and niche differentiation, although recruitment from a local reservoir of

species is acknowledged as secondary explanatory factor. Environmental variability includes both horizontally and vertically variation; and variation between seasons, at the short- and long-term temporal variation. A wide range of mixed C/S/R-strategies are supposed to have evolved at all viable levels and combinations of disturbance- and stress intensity. So, the climatic- and chemical environment of the organism acts as a spatially and temporally changing sieve, which selects for the best fitting set of life history traits at that location and at that moment in time. Although dispersal is recognised as a locally important factor in the CSR theory, the existence of a persistent seedbank, persistent seedlings and vegetative expansion makes that dispersal is ultimately of minor importance to explain species co-existence in most situations (Grime 2001). Hence, it is considered unlikely that the sequence of secondary succession is determined by different colonisation rates but rather by different growth rates ((Grime 2001), p. 242). As growth rates are determined by habitat productivity, the potential productivity of the habitat is considered the main factor determining the relative importance of the different strategies ((Grime 2001), p. 246). The procession of life history strategies that follows a disturbance starts with ruderals that quickly colonise the skeleton habitat, competitors take over because of their much higher resource capture abilities, followed by stress-tolerant competitors and pure stress-tolerant strategies as both nutrients are increasingly hoarded by the biomass and shade is deepening. Competitors thus play and important role in succession at highly productive sites, but at sites with very low productivity they may be dismissed entirely so that stress-tolerators directly take over from ruderals. Species diversity, and hence the opportunity for co-existence, is therefore also assumed to be closely related to the productivity of the site. Along a standing crop axis, low standing crop is explained by either high levels of stress, i.e. in habitats with very few available resources, or by frequent disturbances. At high levels of standing crop, i.e. at sites with high productivity, only few robust and competitive species are able to survive the intense competition. Consequently at intermediate levels of standing crop, i.e. productivity, species representing all strategies are able to maintain in the species assemblage. High diversity and high productivity are thus highly correlated. However, this is for entirely different reasons as Tilman postulates. Tilman's explanation is that with increasing diversity, resource capture is nearly complete and competition is most intense. Grimes explanation is that spatial and temporal heterogeneity of the environment creates a complex mosaic of microhabitats, allowing a broad suite of strategies to co-exist and because the intensity of competition takes intermediate values only. The dominance of these co-existing explanations of the same phenomenon is still an unresolved issue, though both authors may disagree.

4.1.3   *r* − *K* theory

In much of the ecological literature since MacArthur and Wilson (1967) is nonequilibrium dynamics associated with '*r*-strategists' and equilibrium dynamics with '*K*-strategists'. Life-history traits that characterize a pure *r*-strategist include: early senescence and fast development, thus short life span; early reproduction, semelparity and little investment per individual offspring. The life history traits that

characterize a pure *K*-strategist are the opposite, including: late senescence, slow development and thus long lifespan; delayed reproduction, iteroparity and high investment per individual offspring (Pianka 1970). The rationale for the assumed association between the parameters of the logistic equation and the transient (nonequilibrium) vs. competitive (equilibrium) dynamics of species with these life history complexes is provided by MacArthur (1962). He showed mathematically that selection pressure on *r* declines with density, and increases on *K* with increasing density. Selection pressure is defined as the rate of change in fitness with the change in some life history trait parameter. For a continuous time model like the logistic equation, fitness is measured as the relative growth rate, *dN/Ndt* (Caswell 1982). Thus, selection pressure on *r* equals *1-N/K* which declines to zero with increasing density, *N*, and selection pressure on *K* equals *rN/K²* which approaches *r/K* with increasing density. Thus indeed nonequilibrium species are *r-* selected and equilibrium species are certainly *K*-selected (Caswell 1982). The question, however, is the converse: that *K*-strategist *must* be at equilibrium species and *r*-selected strategist *must* be nonequilibrium species (Caswell 1982). The converse proves to be invalid (Caswell 1982). The analysis is as follows.

Two general patterns of demographic patterns of nonequilibrium populations can be discerned. Firstly, one that spends most of its evolutionary history increasing in density and that is periodically eliminated by disturbances. Secondly, one that first rapidly increases in density after colonizing a new patch, but subsequently spends most of its evolutionary history decreasing in density as its abundance is increasingly suppressed by other incoming species at the patch. In effect, in the latter situation the carrying capacity of the site is continuously decreasing. Both for a age-structured matrix model and for a demographic model, Caswell (1982) showed that for an increasing population there is selection on *r*-traits, including early survival and reproduction Whilst for a declining population there is strong selection to increase the mean age of reproduction, the age at which reproduction declines, the span over which reproduction occurs and, to a lesser extend, the gross reproductive rate. As a matter of fact, the patterns favoured in an equilibrium population are even more intensely favoured in a nonequilibrium population which spends most of its evolutionary history in a state of population decline (Caswell 1982). The dichotomy between *r-* and *K*-strategists is thus not so much caused by populations in nonequilibrium and that in equilibrium, respectively, but in the demographic population pattern. Since the traits that increase the time before the population becomes extinct and those that increase the time which a population spends in decline are the same, the *K*-strategists will occupy relatively stable habitats and *r*-strategist more disturbed sites (Caswell 1982).

4.1.4   Nonequilibrium theory

In nonequilibrium terminology disturbances push communities in a state far from equilibrium. Competitive exclusion is then prevented by fluctuations in space and time of the physical environment by disturbances, biotic processes such as herbivory and predation, and environmental constraints like resource status of the soil and drainage patterns (Pickett 1980; Wu and Loucks 1995). Differences in diversity

between communities can then be explained by variations in the rate of competitive replacement of the species, while competitive ability and niche partitioning are of less importance (Huston 1979). The frequency of the disturbance is a first determinant of co-existence. If very high, the system is reset after a short period of development and the community is comprised of a few species with high colonizing ability. If very low, competitive exclusion proceeds to its full extent and few competitive species that are most competitive constitute the species assemblage. Consequently, species diversity is highest at some intermediate disturbance rate that includes the whole range of colonist to competitors simultaneously (Horn 1974; Huston 1979).

4.2   Hierarchy of scales

Nonequilibrium concepts on space, time and scale are important additions to ecological theory. The unit of space is the patch, defined as a relatively discrete spatial pattern that may vary in size, internal homogeneity and discreteness (White and Picket 1985). It may even be submersed or 3-dimensional when applied to aquatic systems. Importantly, patches are characterized differently for species that differ in life history traits. For example differences in mobility between plants and animals make that they very differently perceive a given environment and its heterogeneity. The organism thus makes its own representations of the environment by means of its receptors and modes to respond to changes. Patches are embedded in a landscape, or seascape for that matter, which is 'a mosaic of patches, the components of pattern' (Urban et al. 1987). Its patchiness can be quantified either in terms of patch types and their relative abundance or in terms of size shape, juxtaposition, connectivity and characterization of their boundaries (Wu and Loucks 1995). The fluctations in space and time of both the disturbances and biotic processes, and the environmental constraints are interwoven in landscape development and yield complex patterns. This complexity is organized in special way because size and frequency of disturbance events are positively correlated: low-level events occur comparatively frequent and are small, while high-level events are large and happen only occasionally (Urban et al. 1987). Dynamics of the higher hierarchical scale is a composite of lower scale dynamics and their interactions (Wu and Loucks 1995). E.g., population dynamics and extinction operates at the patch scale, this affects metapopulation dynamics at the landscape scale and, for aspect determining species, this dynamics affects energy flows and material cycling at the ecosystem scale. Vice versa, higher spatial scales pose constraints on the lower levels. For instance, the rate of material cycling constrains the rate of succession and thereby dynamics of patchiness at the landscape scale and this patchiness provides structural constraints for population dynamics at the patch scale. Hence, pattern, process and scale form an inseparate nonequilibrium trinity. The nonequilibrium trinity is driven by stochastic disturbances which essentially make all relationships ephemeral and all dynamics transient, albeit to a lesser or larger extent.

4.2.1 Incorporation

A new aspect in nonequilibrium thinking, compared to equilibrium thinking, is the recognition that local extinction is a common phenomenon and that migration of individuals or propagules between patches plays an important role in the persistence of a species at larger spatial scales. A zero population size is thereby not a boundary state or endpoint in a nonequilibrium world as it is in an equilibrium one (Caswell 1978). The locally extinct species may contribute to succession later, as long as sufficient migration between patches is possible. A consequence of that recognition is that the ardent discussion on density dependent factors and increasingly complex niche partitioning models to explain persistence of species waned for the simpler and biologically realistic explanation of transient persistence and migration. Or rather, the extent of the validity of density dependent factors was greatly reduced by nonequilibrium theory.

Nonequilibrium patch processes may translate to an equilibrating landscape with a stationary distribution of patch types and –sizes Urban et al (1987). This concept of landscape equilibrium is similar to that of the 'shifting mosaic steady state' of Watt (1947) and Borman and Likens (1979). Indeed a more insightful terminology than the 'homeorhetic quasi-equilibrium' introduced in the nonequilibrium literature (Wu and Loucks 1995). In terms of predictability this means that persistence of a species can have a rather high predictability at the landscape scale, but at the same time have a relatively low predictability at the patch scale. Whether a landscape equilibrates depends on the scale of both disturbances extent relative to the size of the landscape, and of disturbance interval relative to the time to recover to a mature stage (Turner et al. 1993). A disturbance regime can thus be incorporated if steady state dynamics at the landscape scale is composed of transient dynamics at the patch level. New, barren, patches are continuously created by disturbances which at some point cease being open, colonisable patches as succession proceeds. In terms of Turners' scaling of the extent of disturbances with landscape size and interval between disturbances with recovery time, qualitatively 4 combinations of extremes exist (Figure 4):
1) if the disturbance interval is long relative to recovery time and a small proportion of the landscape is affected, the system is stable and exhibits low variance over time. These are traditional equilibrium systems that can attain a predictable climax state in the sense of Whittaker (1953).
2) if the disturbance interval is comparable to the recovery interval and a large proportion of the landscape is affected, the system is stable but exhibits large variance. Almost the entire landscape is reset and homogenized occasionally and secondary succession can restart. The trajectory succession takes is, however, not very predictable as pre-emptive utilization of resources, especially space, by a species will be largely stochastic and determine the rate of subsequent succession over large areas.
3) if the disturbance interval is short relative to recovery time but affecting small portions of the landscape, the landscape is able to incorporate the disturbance regime. This system mimics the 'shifting mosaic steady state' of Bormann and Likens (1979). The predictability will be low at the patch level but at the landscape scale the distribution of patch types and patch sizes may become

stationary in the sense of Urban et al.(1987). Empirical evidence of a stationary patch distribution are, however, hard to find and more resemble a mosaic of nonequilibrium mosaics (Turner et al. 1993).

4) if the disturbance interval becomes much shorter than the recovery time and a large proportion of the landscape is affected, the system may become unstable and shift into a different trajectory. It cannot incorporate the disturbance regime, but the system has high predictability because the transient dynamics are continuously reset to early successional stages.
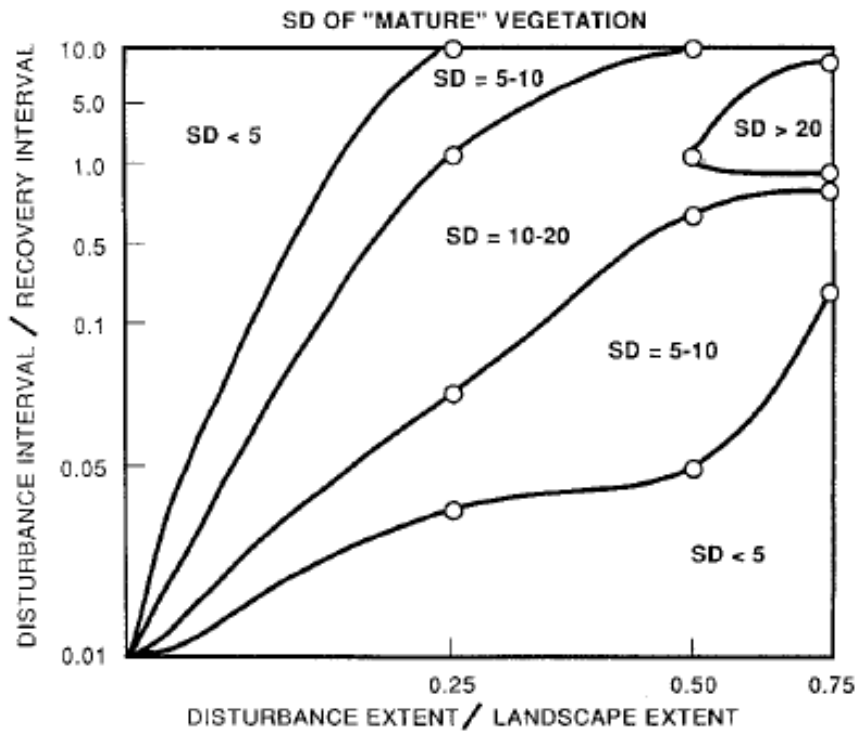
Figure 4. Clipped from: Turner et al. (1993). State-space diagram of the temporal and spatial parameters used to describe potential disturbance dynamics which define the regions of high and low standard deviation (SD) in the proportion of the landscape occupied by the mature seral stage during a simulation of 100 time steps.

4.2.2 Stability and persistence

Remains the question how ecosystems persist in the face of destabilizing forces. DeAngelis and Waterhouse (1987) discern firstly, strong nonlinear feedbacks and time lags cause biological instabilities and secondly, demographic haphazardness and environmental fluctuations cause stochastic instabilities (see Figure 5). Based on that scheme, they proposed 3 categories of ecological communities: 1) stable interactive communities that return to equilibrium values caused by negative biological feedback mechanisms; 2) unstable interactive communities that have one or more unstable states caused by positive biological feedback mechanisms between species and that

result in species extinctions; and 3) weakly interactive communities that are unstable because stochastic fluctuations are stronger than biological interactions and knock the populations away from an equilibrium state, and are stochastically dominated. DeAngelis and Waterhouse (1987) discern 5 hypotheses that ecologist include in their models to explain the question on ecosystem persistence in the face of destabilizing factors, 3 at the patch scale and 2 at the landscape level (see Figure 5, enumeration follows that scheme):

1) *Intrinsic population dynamics stabilizing mechanisms.* This especially includes trophic interaction such as prey refuges, predator searching time, predator interference and predator switching behaviour. Models including such feedback are generally more stable that those without, indicating that May's (1973a) result showing lack of stability in randomly assembled communities does not occur in real ecosystems. Empirical and theoretical evidence is, however, still conflicting, leading DeAngelis and Waterhouse to the conclusion that ecological theory cannot be based on inherent stabilizing mechanisms only.

2) *Disturbances as stabilizing factors in feedback dominated systems.* By his much cited 'paradox of the plankton', Hutchinson (1961) explained co-existence of plankton species by ongoing disturbances that prevent competitive exclusion to take its full course, because niche differentiation cannot explain the persistence of so many species that utilize so few limiting resources. Extensive research on the intermediate disturbance hypothesis (Huston 1979); on disturbances affecting either population numbers or their resources; and model studies on red and white noise on either growth rates or carrying capacity (see above) all belong to this area.

3) *Persistence of stochastically dominated systems through biotic compensatory mechanisms.* Such a mechanism can be that in a landscape, whose dynamic is characterized by frequent disturbances, a 'floor' of good habitat is stably present. These sites act as a haven for the species or 'secure habitat sites'. The ceiling of the population is determined by the occupancy of poor habitat that becomes available as succession develops and by increasing intraspecific competition. The species is then occasionally erased resulting in large stochastic fluctuation in population size.

4) *Weak coupling of feedback of unstable cells in a landscape.* If the cause of instability is by biological feedbacks that operate at the local scale, extending the scale of the study may solve the issue of persistence. Persistence then depend on whether the landscape can incorporate a disturbance regime, as discussed by Turner et al. (1993) (see above).

5) *Weak coupling of stochastically dominated cells in a landscape.* Also, if domination of stochastic factors on local population fluctuations may be largely avoided if the issue is studied on a larger spatial scale. Similarly as with destabilizing biological feedback, do spatial extent and heterogeneity with steady migration between patches act as stabilizers at the level of metapopulations.

See DeAngelis and Waterhouse (1987) for references on theoretical and empirical studies on each of these proposed mechanisms.
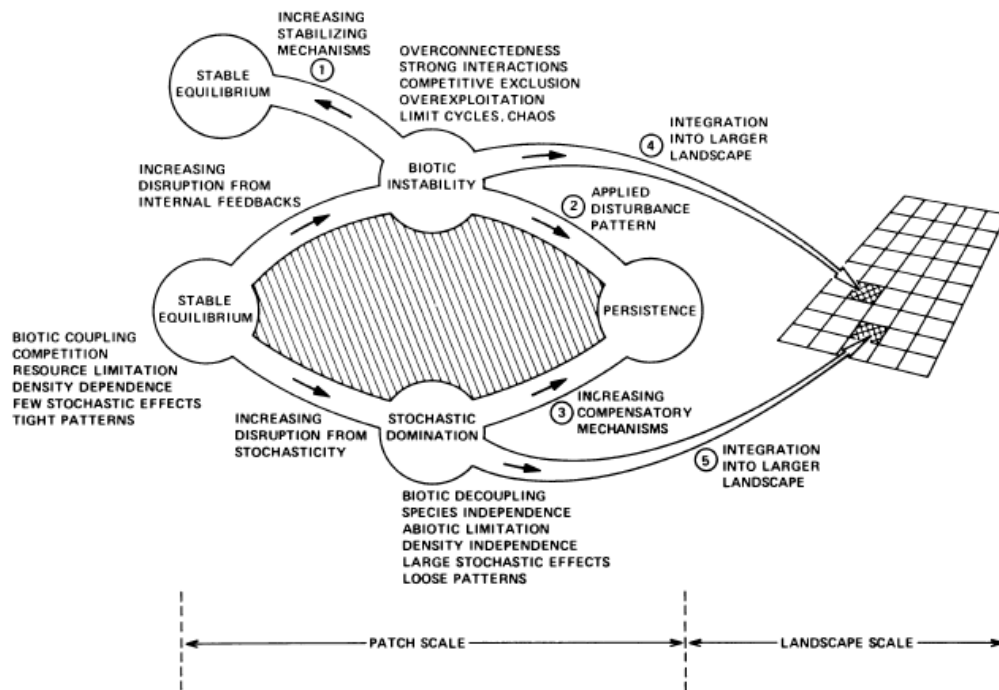
Figure 5. Clipped from: (DeAngelis and Waterhouse 1987). Accompanying text: "Diagram showing 5 general types of hypotheses to explain why ecosystems can be stable despite the prevalence of biotic instabilities and environmental stochasticity."

In summary, as dynamics are transient it is the persistence of species that is the prime focus of nonequilibrium research. Transient dynamics imply that stability is only of interest at the next higher spatial or temporal scale. The role of disturbances, that are stochastic by definition, drive the dynamics at all scales depending on extent and frequency relative to the area of interest and the rate of response of the system, respectively. A disturbance regime can be incorporated if the relative extent and the relative response time take intermediate values, thus defining the nonequilibrium notion of stability. Any system will possess stability at some scale, so that the appropriate scale should be sought after to assess the predictability of successional pathways.

4.2.3 Resilience and adaptive capacity

In nonequilibrium theory the concept of resilience takes a different meaning than in equilibrium theory. Holling (1973) reflected on the different ecological world views that are encapsulated in either in the idea of transient persistence of individuals, populations and species. They die, disappear and become extinct. Or in the idea of constancy of their numbers, that should return to a stable value after a small perturbation. The former is a qualitative concept whilst the latter is quantitative. The relevance of these visions depends on the functioning of the system. If a system is

continuously confronted by the unexpected, the constancy of its behaviour becomes less important than the persistence of the relationships among its members. If, on the other hand, the system operates under a narrow range of predictable external conditions, the concern is on the counteractions the system undertakes following critical events to attain the stable state again (Holling 1973). Holling finds that ecosystems do operate in a unpredictable and stochastic world and are likely to be continually in a transient state. He therefore introduced a concept of resilience that accommodates for random events and spatial heterogeneity which bring ecosystems beyond the arena where stability analysis is applicable. He describes resilience as follows (Holling 1973):

> "Resilience determines the persistence of relationships within the system and is a measure of the ability of these systems to absorb changes of state variables, driving variables, and parameters, and still persist. In this definition resilience is the property of the system and persistence or probability of extinction is the result."

Accordingly, resilience can technically be defined as the size of the basin of attraction around a stable point, *i.e.* the width of the stability domain (Scheffer and Carpenter 2003) (See Figure 1). If pushed around within the basin, either by large random events, by gradual environmental changes or by human impacts, the persistence of relationships make that the system returns towards the attractor but may fail to reach that point before the next random event happens. Still, the system is resilient in its relationships. If pushed outside the basin it isn't, and will follow a different trajectory. Resilience is measured by the magnitude of the disturbance that the system can absorb before it changes stable states, hence before it redefines its structure by changing the variables and processes that control its behaviour (Gunderson 2000). In the heuristic scheme of Scheffer et al. (2001) resilience is represented as the width of the cup and mediates between alternate basins of attraction (Figure 2).

However, the size and shape of the cup are not fixed. Internal dynamics but also human induced impacts like climate change affect key variables that determine the stability domains of the system (Figure 1). The *adaptive capacity* of the system represents this change of stability landscape and change of the size of the basins of attraction of alternate attractors (Scheffer and Carpenter 2003). Holling (1992) provides an abstract representation how adaptive capacity and thereby resilience changes during an ecosystem succession (Figure 6). The equilibrium functions of ecosystem succession include *exploitation*, with rapid colonisation of recently disturbed areas, which is passed on to *conservation* during which there is a steady accumulation and storage of material and energy in the system. Succession proceeds as species that win the scramble competition are replaced by species that are the better exploitative competitors in a predictable procession as reviewed by Horn (1974). Nonequilibrium functions then set in as the system becomes increasingly fragile, i.e. sensitive to a large scale disturbances that *releases* the build up material and energy, this subsequently leads to a *reorganization* in which soil processes and immobilization minimize nutrient loss and reorganize nutrients to become available for the next phase of exploitation (Horn 1974). Ad infinitum.

The ability of the system to reorganize and renew depends on dynamics at the hierarchical scales above and below the disturbed one (Folke et al. 2004). This means

that the scaling of extent of disturbance and of disturbance interval as proposed by Turner et al. (1993) is an important addition to make the scheme of 4 alternating ecosystem functions operational for actual ecosystems.
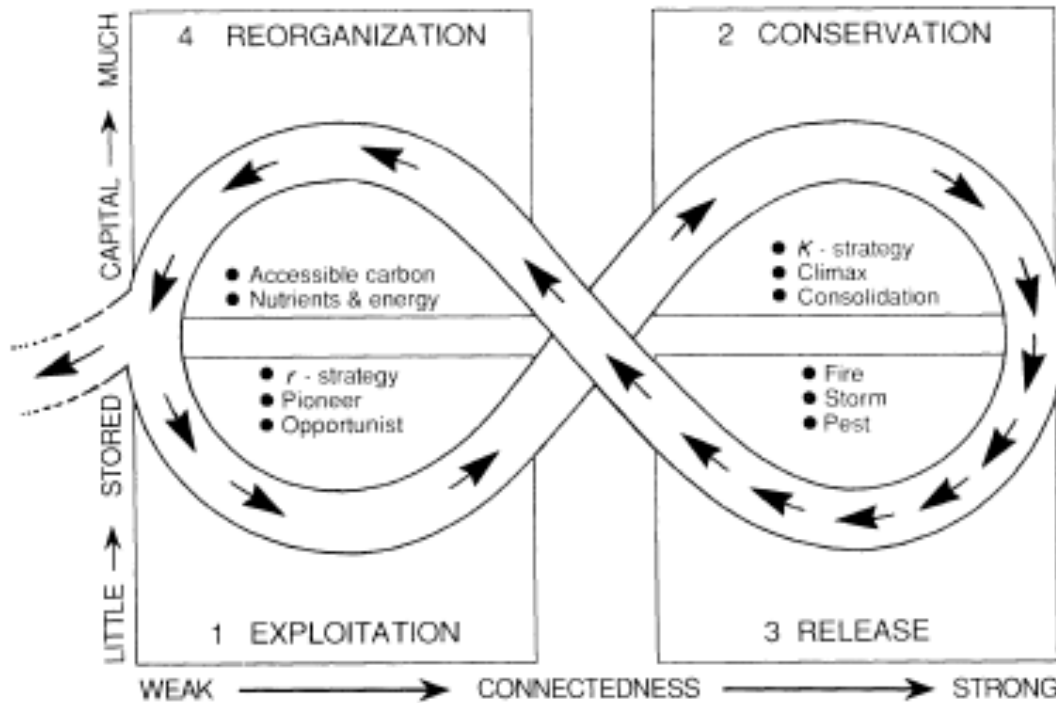

Figure 6. Clipped from Holling (1992) Accompanying text: "The four ecosystem functions and the flow of events between them. The arrows show the speed of that flow in the ecosystem cycle, where arrows close to each other indicate a rapidly changing situation and arrows far from each other indicate a slowly changing situation. The cycle reflects the changes in two attributed, i.e.. (1) Y axis: the amount of accumulated capital (nutrients, carbon) stored in variables that are the dominant keystone variables at the moment and (2) X axis: the degree of connectedness among variables. The exit from the cycle indicated at the left of the figure indicates the stage where a flip is most likely into a less or more productive and organized system, i.e.., devolution or evolution as revolution!"

Because resilience in nonequilibrium theory concerns the persistence of relationships it focuses its attention to ecosystems functions that in many cases are translated into services for human societies. Thus rather than addressing taxonomic diversity expressed in species richness and evenness (Naeem and Wright 2003), functional aspects of diversity are discerned that appear to be critical for ecosystem resilience. Such functional aspects include *functional group diversity* and *functional response diversity* (Folke et al. 2004). Functional groups are groups of organisms such as pollinators, grazers, predators, nitrogen fixers, seed dispersals, decomposers, species groups that generate soils, modify water flows, groups that that open up patches for reorganization, or contribute to the colonisation of such patches (Folke et al. 2004). Functional response diversity refers to the plethora of responses to environmental change among species that contribute to the same ecosystem function (Elmqvist et al. 2003). Variability in responses of species to environmental change within functional groups is critical to ecosystem resilience as they appear to be largely redundant for ecosystem functions, like productivity. Differences in environmental

sensitivity among functionally similar species therefore give stability to ecosystem processes, whereas differences in sensitivity among functionally different species make ecosystems more vulnerable to environmental change (Chapin et al. 1997). A loss of species that have similar ecosystem effects but differ in their environmental responses may therefore reduce he ecosystem resilience and the adaptive capacity to adjust to environmental changes (Chapin et al. 1997). As species replace each other over time depending on the nature of the environmental change, they ensure maintenance of that function over a wider range of environmental conditions than can be coped with by any single species. This replacement does not need to take a linear course, thereby allowing the species to co-exist in a temporally changing environment. Redundancy in diversity then operates as an insurance as high response diversity increases the likelihood for renewal and reorganization into a desired state after disturbance (Elmqvist et al. 2003).

The dichotomy in functional group diversity and functional response diversity translates into life history traits where *effect traits* need to be discerned from *response traits* (Naeem and Wright 2003). Effect traits contribute to the ecosystem function being measured. E.g. denitrification, nitrification, ammonification are effect traits if soil nutrient status is the object of interest (Naeem and Wright 2003). Response traits on the other hand, determine the system's response to environmental changes. Research on the relationship between biodiversity and ecosystem function then address the role of species traits in ecosystem functioning, the distribution of functional traits in species assemblages, and the use of abiotic variables of biodiversity such as disturbance regimes and other factors (see (Naeem and Wright 2003) for a research program on this approach).

Note that although the terminology in either effect and response traits at the species level of Naeem and co-workers coincides with the functional grouping of species based on effects or responses traits, the ecosystem functions that are addressed appear not to coincide fully. For Naeem ecosystem functions refer to biogeochemical activities including the flow of nutrients, water and atmospheric gasses and the processing of energy (Naeem 1996). Whereas the definition of Holling refers to the more abstract notions of exploitation, conservation, release and reorganisation (Holling 1992).

4.3   Equilibrium or nonequilibrium: 2 ecological world views

The 2 ecological world views, that either assume constancy and the balance of nature or that nature is inherently uncertain and unpredictable, may clash if applied to conservation management. It is conceivable that the probability of local extinction of some species increases if managed on constancy, *e.g.* for fish populations to provide a maximum sustainable yield, or for a watershed to supply a non-fluctuating amount of water (Holling 1973). Isolation and a 'command and control' approach of management for specific variables of interest can result in the erosion of resilience (Gunderson 2000). This approach of management is valid if it can be assumed that the system operates near equilibrium and the control is sufficiently large so that deviations from equilibrium can be restored. For example, to maintain biodiversity in a fine grained and diverse traditional agricultural landscape with cultivated grasslands

which have a long history of locally constant management. Resilience, expressed as return time, is then improved by technological solutions which are invented by a disciplinary science.

More natural ecosystems, on the other hand, are prone to inherently unpredictable events which cause a 'resource crises' in the management of the system. Resilience, expressed as the system's ability to absorb those events, requires the occurrence of disturbances as otherwise the species that enable the renewal of the ecosystem in the first place, are lost. The management paradigm that considers surprises as inevitable and finds that knowledge is always incomplete, is that of *adaptive management*. Adaptive management aims at developing strategies that: 1) increases the buffering capacity of the system. By allowing small scale perturbations to operate to avoid large scale disturbances; 2) manages for processes at multiple scales; and 3) nurtures the sources of renewal (Gunderson 2000). The adaptive management approach focuses on 'learning by doing' (Folke et al. 2004), but it must be noted that currently few examples exist from which adaptive management indeed can be learned.

The meaning of resilience is thus drastically different in equilibrium- compared to nonequilibrium thinking. Moreover, the concept of *predictability* appears to have changed. Equilibrium theory focuses on predicting the future thereby trying to improve *chronological predictability*. Nonequilibrium theory addresses the conditions for systems that have qualitatively the capacity to absorb and accommodate unexpected future events and attempts to assess its *logical predictability* ((Mayr 1997), p.53). Scientific concepts appear to have diverted indeed between equilibrium and nonequilibrium theory which has important consequences for conservation management. While a change in paradigm is a slow and confusing process in science, this is even more so if paradigms have been adopted in the political and societal arena. This appears to be the case for nature conservation and -management.

5 Research program on ecological succession for conservation management

5.1 Research questions

A crucial research question that needs to be addressed to support nature conservation management is: What is the role of biodiversity for ecosystem functioning in general and in particular for its resilience to whatever factor affecting it? I.e. how to maintain and restore resilience for ecosystem functions in environments that are affected by local and global changes? The analysis of that question involves a number of steps:

1. The importance of biotic interactions among organisms and between organisms and the environment, versus that of the importance of stochastic events that operate at multiple scales and frequencies must be analysed for particular ecosystems. Of particular importance is the strength of the interactions between organisms and resource availability as that results in the possibility that an ecosystem can exist in alternative stable states at the same resource availability. Biodiversity could be such a factor for some systems, but also other factors that show positive interaction between resource availability and ecosystem functioning should be evaluated for the existence of multiple stable states.

2. The analysis should be based on the distribution of life history traits among species in an assemblage. This considers both effect traits that contribute to the ecosystem process of functions being measured and response traits that determine the response of species to environmental change. It should be determined if species with similar effect traits for particular ecosystem functions have a wide variety of response traits to environmental change. If so, this would indicate resilience to environmental change and temporal stability at the community level.

3. Disturbance regimes need to be characterized in relation to the distribution of life history traits over the local species pool. The extent of a disturbance should be characterized in terms of dispersal distances and it needs to be analysed if the distribution of disturbances that differ in extent matches with the distribution of the extent of disturbances. Similarly, for the frequency of disturbances it should be determined how the return time is based on fecundity and mortality of the local species pool.

The previous analyses then allows the categorization of ecosystems in the scheme of DeAngelis and Waterhouse ((1987), see Figure 5) and to refine he research for the functioning of that particular ecosystem. Research questions, and related ecosystems, then fall in the following broad categories:

On stability. Equilibrium theory is confined to a specific scale and to small deviations from equilibrium so that strong biotic interactions determine the return time towards the attractor state. The return time is mainly explained by resource limitation and density dependent factors that need to be quantified to assess ecological succession and species co-existence. If a particular system can be considered rather stable, in terms of neighbourhood stability, it needs to be found out which intrinsic population

dynamics operate as stabilizing mechanisms and at which scale. Trophic interactions, including herbivory and predator-prey interactions are then the main focus of attention to assess the predictability of the system under study. Additionally, stochastic effects are small in order that the system maintains its functioning and ability to return quickly to equilibrium. The extent and frequency of these stochastic events thus need to be quantified.

On biotic instability. Strong biotic interactions may lead to competitive exclusion and overexploitation of resources and consequently lead to strongly fluctuating, hence largely unpredictable, population dynamics that possess limit cycles, which circle around an attractor state without ever reaching it, and possibly chaos. If a particular ecosystem is unstable because of strong biotic interactions, the role of biodiversity to provide stabilizing mechanisms is the main focus of attention.

On stochastic domination. Increasing stochastic disruption leads to decoupling of species interactions. This means that density dependent interactions are made in-operational and that the ecosystem dynamics are independent of abiotic resources. Ecological succession and co-existence of species is thus largely explained by the occurrence of large stochastic events and by the dispersal and colonizing capacity of the species. The focus of research is then on the nature of the disturbance regime and the recovery time in relation to life history traits of the species pool.

On persistence. Systems that are instable due to strong biotic feedbacks may be stabilized by disturbances so that species are able to persist as a consequence of spatial and temporal heterogeneity. Similarly, species persistence is possible in stochastically dominated systems through compensatory mechanisms like secure habitat types. Integration of biotic or stochastic unstable patches into a larger landscape is critical for conservation management. Disturbance regimes then need to be characterized relative to the size of the landscape and the recovery time of the system after disturbance. The scaling of extend and frequency of disturbances is then a prerequisite to assess the dynamics in those systems.

5.2 Approach

The predictability of ecological succession will not be the same for each of these categories of ecosystems. Nonequilibrium, process-based models that operate at the landscape scale and that include realistic disturbance regimes are the only means to analyse these issues. For terrestrial ecosystems, such models are available (e.g. the WETSPACE model for grazed highly productive meadows and marshlands (Groot Bruinderink 1999) and the FORSPACE model for dynamics of forested landscapes, including fire regimes and its feedback with the vegetation (Kramer et al. 2003b; Kramer 2001), and that can also be applied to dune ecosystems). For fresh water and marine ecosystems nonequilibrium ecosystem models may still have to be developed. Realistic disturbance regimes must be further be developed for such models. The main challenge is then the characterization of species, and the grouping of species in functional groups, so that species diversity and the persistent presence of target species in the landscape can be assessed without having to explicitly model each and every individual species. Such complex models should be developed with a close link and simultaneous development of minimal models that allow analytic evaluation of

key-processes and the existence of multiple stable state. So that the minimal modes provide the analytical insight and the complex model the realism of the existence of thresholds between alternate states. Based on the above mentioned protocol, realistic targets and timeframes should be formulated for the conservation management of particular ecosystems.

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Part II. Examples and application of the theory for the management of aquatic and terrestrial ecosystems

In the previous section the general biological concepts and principles on ecosystem succession and its predictability are described. For different ecosystems, however, variants of the general concepts have been developed within the different biological fields, each with their own specific research questions. These different ecosystems will be considered in the following section focussing firstly on aquatic ecosystems including freshwater and marine ecosystems, and secondly on terrestrial ecosystems, including dune and forest ecosystems.

7 Fresh water ecosystems

Piet Verdonschot

7.1 Co-existence and ecosystem dynamics

Rivers and streams can be physically harsh environments in which organisms are frequently at risk of being swept away in the currents. Floods may remove substrates partly or entirely and cause temperature and oxygen stress, whereas droughts and dewatering can result in particular harsh environments for aquatic organisms. The question if then: is a stream therefore either a harsh environment for the organisms living there so that the prevalent environment determines the occurrence of species; or are these organisms adapted to the harsh conditions they occasionally experience and is their co-existence essentially explained because they form strong interacting networks? This question has a long standing debate in aquatic ecology. Examples for the latter view include the evidence for differences in functional fish assemblages related to flow variability (Poff & Allan 1995), for aquatic insect in relation to seasonal variation in flow by Flecker & Feifarek (1994). Seasonal extreme flash floods resulted in the co-existence of two fish species (Meffe 1994) and of two insect groups (Hemphill & Cooper 1983).

The importance of biotic and abiotic processes and their mutual weight on the observed ecosystem is influenced by the observer. In an equilibrium view the observed community pattern is the result of interactions amongst species. In the nonequilibrium view the role of dynamic environmental processes are of greater importance.

Equilibrium concepts in aquatic ecology include:

- *Lottery system* (Sale 1977): all species are competitively equivalent, and dominance between species shifts according to changing environmental conditions and the life-span of component species.

- *Competition based concepts* (niche controlled communities): coexistence is attributed to species differences along resource or habitat axes, and abiotic factors are of little importance (e.g. Yodzis 1986, Townsend 1989).
- *Successional sequences (including the dynamic equilibrium model)*: during succession colonists are replaced by superior competitors (Fisher et al. 1982).
- *Habitat template* (Southwood 1977): the multitude of ecological strategies arise from evolutionary trade-offs of cost versus benefits in the process of adaptation to habitats.

Whereas nonequilibrium concepts in aquatic ecology include:
- *Harsh-benign concept*: biotic processes are not able to convey regularity and structure to communities when environmental conditions fluctuate and both exist near each other in streams (e.g. Peckarsky 1983).
- *Patch dynamics concept* (Patrick 1975, Townsend 1989): disturbance frequently removes organisms and opens up space which then can be colonized by individuals of the same or different species (under the assumption that in streams habitats show a patchy distribution in space and time and the organisms show a high dispersal ability thus emphasizing differences in life-cycles and colonization abilities of the individual taxa). Consequence is the predictability of the overall mosaic of environmental conditions.
- *Intermediate disturbance hypothesis* (Ward & Stanford 1983): greatest diversity occurs under conditions of intermediate disturbance, because good competitors and good colonizers both are represented (competitive ability is hierarchical (see McAuliffe 1984b) and inversely correlated with colonizing ability) (Connel 1978)

At the habitat scale, the *Habitat template* and the *Patch dynamics* concept deal with the species and their biotic and abiotic interactions. Both deal with diversity and support nature conservation. The concepts dealing with habitats and patches in streams can be applied in two ways. Firstly, there is a relationship between patch dynamics and diversity as well as between *K*- and *r*-strategies and adverse taxa. Diversity depends on the relation between temporal and spatial variability. Secondly, these concepts most probably can be used at higher scales as well, e.g. landscapes. This has not yet been tested and requires further research.

7.2   Hierarchy of scales

At the landscape scale, natural stream valleys compose heterogeneous landscapes. Aquatic species show heterogeneous distribution patterns as each of them depends on different abiotic and biotic environmental factors. An aquatic species does not occur at a site because of site specific features but also because of the environment around such site (Moller-Pillot 2003). Each species uses this environment in a different way. A species can only occur sustainable in an area if the landscape is suited to fulfil the species complete life-cycle. But it won't be present at each suited site all time. Thus ecological similar sites will differ in their overall species composition. Furthermore, species will not only occur within their optimal habitat but also survive under less optimal conditions (e.g. Hall et al. 1992), illustrated by 'source' and 'sink' habitat (Pulliam 1988). 'Sinks' are insufficient to sustain long term

survival and 'sources' are needed to supplement specimens. Landscape heterogeneity is a component that adds to the predictability of a community composition. It shows the increase of unpredictability at the small habitat patch scale and stresses the importance of the neighbouring environment.

Hierarchy theory provides a framework for describing the components of an ecosystem and their scaled relations (O'Neill *et al.* 1986, Jensen *et al.* 1996), which can characterized for freshwater ecosystems as as follows:
(1) Every component of a stream is a whole and a part at the same time (the whole/part duality).
(2) Patterns, processes and their interactions can be defined at multiple spatial and temporal scales (Levin 1992) and are interwoven (Hutchinson 1953).
(3) The relationship between ecological processes (and the patterns they create) changes with spatial scale (Turner 1990).
(4) Levels of ecosystem organisation at coarser scales bound the range of ecological properties that emerge at finer scales (Allen *et al.* 1984). At the same time, finer scales to a lesser extent affect coarser ones (e.g. 'top down' and 'bottom up' control of food webs; feedback loops, Costanza *et al.* 1993).
(5) No single scale of ecological organisation is correct for all purposes. This is important because more often only information at one or a limited number of scales is provided.
(6) The definition of an ecological hierarchy (component patterns and processes) is always dictated by the objectives of a study.

The multitude of processes that form stream systems can be considered as a hierarchical framework (Allan & Starr 1982, Frissell *et al.* 1986). Indeed, large watersheds are comprised of tributaries and their catchments. Tributaries contain multiple stream reaches; each reach potentially includes riffles, pools and other habitat units, and these habitat units each contain multiple microhabitats (Frissell *et al.* 1986, Sedell *et al.* 1990). Hence, Ward (1989) introduced the concept of the four-dimensional nature of stream ecosystems at the catchment level, recognizing that ecological connectivity has a longitudinal, lateral, vertical and temporal component. These 4 dimensions include:
1. The longitudinal interactions relate to upstream-downstream effects, either seen as a sequence of interlinked zones (Illies & Botosaneanu 1963, Hawkes 1975) or as a longitudinal continuum (Vannote *et al.* 1980, Wallace *et al.* 1977). Hereby, the effect of downstream activities on upstream stretches such as the effect of downstream canalisation on discharge and erosion patterns up-stream (Schumm 1977), or the effect of downstream weirs on migration should not be neglected.
2. The lateral component (Petersen *et al.* 1987, Naiman & Décamps 1990) includes the instream transversal gradient, the link to the riparian zone and the 'dry' area of the catchment. For example, it includes the surface runoff and wind transport of silt and substances towards the stream.
3. The vertical component includes the groundwater flow (Brunke & Gonser 1997) and the hyporheic community (Stanford & Ward 1988), but also the exchange between stream and air, such as evaporation and deposition of substances (e.g. Kristensen & Hansen 1994) and the terrestrial phase of insects.

4. The temporal component, such as the organism's life history, the processes of meandering (Boon 1992), and the patch dynamics (Townsend 1989), also include historic developments (Kondolf & Larson 1995).

The concept of *"four-dimensional nature of lotic systems"* identifies all interactions and the functioning of the stream as an integral part of the whole catchment. It considers streams as open ecosystems and as such it can be used as a frame for integrated water management. Several concepts deal with the effect of stream hydrology on the functioning of the stream and its direct surroundings, i.e. the longitudinal and lateral interactions as a whole. These concepts deal with stream functioning as a whole at the same time imply a more or less gradual shift in species composition along the stream gradient. Implementing hierarchy theory in the description of catchment ecosystems thus involves explicitly characterising the scaled relations between the patterns of interest; the ecological factors (processes) that determine these patterns; the spatial and temporal bounds of each; and the order in which they are nested. The smallest resolvable area (grain), the area influenced by the phenomenon under study (extent), and the boundaries of the respective system, determine the scale of observation.

The emerging view is that no single concept can adequately describe all communities. Some are strongly influenced by biotic processes, others by abiotic processes, and the applicability of each of the concepts is situation-specific. The harsh-benign hypothesis is likely of importance at a local scale where chance and a fluctuating environment are of considerable importance (Fleckker 1992b). The competition based models only account when environmental conditions are relatively constant and strong biological interactions may convey considerable regularity to the composition and relative abundance of species in an assemblage. However, the patch dynamics model in which environmental unpredictability interacts with species-specific differences in life history characteristics and dispersal ability, may frequently play the largest role in governing the make-up of stream communities.

8 Marine ecosystems

Bert Brinkman

Predicting the behaviour of marine systems is basically different from most terrestrial systems. A main problem is that almost everything is mutually related. The behaviour of, for example, the ecosystem of the Dutch Wadden Sea cannot be separated from the conditions in the adjacent North Sea. On its turn, the North Sea behaviour is strongly linked with the North Atlantic, and with that, the global ocean system comes into view. Related with this characteristic is that the relevant processes or state variables are very hard to study. Fish is hard to monitor during its life cycle, and those organisms that can be studied, like Wadden Sea shell fish undergo so many kinds of influences like food availability, temperature and predation that field observations are hard to interpret. Where in terrestrial systems field experiments can be conducted the marine researcher has to stick to laboratory experiments whose results are hard to translate to the 'real world'. Globally one may say that predicting marine system behaviour is limited to a certain level of detail. Predicting the whole system functioning in terms of primary and secondary production, related to e.g. temperature, nutrient inputs, stratification may be achieved. These predictions are limited to the magnitude of these processes, and do not tell us anything about species. And usually, there is a major step needed *before* one comes to such an ecological overall picture, and that concerns the physical part. There is no ecological model of the ocean, North Sea or Wadden Sea without a physical background: flows, dispersion and vertical mixing characteristics have to be available before any ecological computation can be successful. Models describing ecosystem functioning can be divided into two major groups: equilibrium models and nonequilibrium models. Though equilibrium does not occur in real life, one may regard the average condition of a system. Such equilibrium –or steady state- models describe the average flows of matter through a food chain.

8.1 Ecosystem functioning: whole system descriptions

8.1.1 Equilibrium (or: steady state) models

Basically, one may consider an ecosystem as a system that is highly dynamic. On the other hand, all types of functions are performed by the available organisms, and these all have to match the overall law: accumulation = input minus output. And the transformations by all organisms have to fit. Thus, one is able to describe an overall food web picture, and assign flows from each functional part into all other functional parts, with a matching overall budget. All the defined flows have to be (can be) quantified –although sometimes with a very large uncertainty- and as a result the impact of natural or human activities can be estimated.

The EcoPath-EcoSim models are a major model example (Christensen and Pauly 1992, Pauly *et al.* 2000). The website explains it as follows:

> *"The foundation of the EwE suite is an Ecopath model (Christensen and Pauly 1992, Pauly et al. 2000), which creates a static mass-balanced snapshot of the resources in an ecosystem and their interactions, represented by trophically linked biomass 'pools'. The biomass pools consist of a single species, or species groups representing ecological guilds. Pools may be further split into ontogenetic (juvenile/adult) groups that can then be linked together in Ecosim. Ecopath data requirements are relatively simple, and generally already available from stock assessment, ecological studies, or the literature: biomass estimates, total mortality estimates, consumption estimates, diet compositions, and fishery catches."*

Human impact, like e.g. fishery, affects certain parts of the food web, and allow (or better: force) other organisms or groups to take over their functioning, since the mass budgets have to be met. The primary advantage of steady-state models is that the most relevant parts of the whole ecosystem food web are covered and (semi-)quantified. The second advantage is that any difficulty regarding model stability, a major problem of dynamic models, is avoided. The quantification if flows and stocks or estimate of the quantities allow us to perform a kind of scenario studies, with fishing as a major human activity. Since the relationships used in the model basically are not functional, any resource competition nor any species specific response to changing conditions is out of the question. Pauly et al (2000) used this modelling tool for their analysis of fishery effects on ecosystem ("fishing down the ecosystem").

8.1.2 Dynamic (nonequilibrium) models

Most of the dynamic ecosystem models cover the factors mentioned above (whole system functioning related to e.g. transport properties, temperature, nutrient inputs and stratification) and are able, to a certain level, to compute primary and secondary production in tidal, shallow non-tidal and deep stratifying systems. Overall flows as mentioned in the steady state models above may be covered as well, but the model may become unstable when species or functional groups show resource competition characteristics, and might out-compete each other. Therefore, most ecosystem models are restricted to an overall description of primary and secondary production, based on a limited number of functional groups (nutrients, algae, secondary producers, detritus with or without bacteria and sometimes fish). The stability of the model results becomes less with increasing complexity of the model, and increasing level in the food web.

Thus, the ecosystem model prediction concerns something what might be called a *normal operating range* for both production processes. This is what the ERSEM model for the North Sea ecosystem does (Baretta et al, 1995), and this is what the EcoWasp ecosystem model for the western Dutch Wadden Sea does (Brinkman & Smaal, 2003).
The Delft Hydraulics Bloom phytoplankton model (see Moll & Radach, 2003) does compute an optimal species composition for the algal community as a whole, but the

species are virtual ones (functional groups), each reflecting certain affinities for some nutrients, light and temperature.

Such dynamic models are useful as a tool when the effects of e.g. nutrient loads or changing turbidity are to be estimated. They are not suitable for studying species specific responses. But, a model that is developed to study the response of competing species to environmental characteristics may use the simulation results of such complex models as boundary condition.

In the case of shellfish fisheries in the Dutch Wadden Sea, model runs made clear that from 1980 and 2000 a decreasing phosphorus input caused a lower maximum shellfish biomass. A part of the biomass really present serves as food for migrating birds, and another part is fished by fishermen. Since the Wadden Sea is a major nature area, and an important link on the east Atlantic Flyway, a decreasing secondary production implies less space for fishermen to harvest from the system. Political consequences are that fish allowances that often contain harvest quota have to be adapted to a new situation.

In the field it can be observed that not only the production is decreasing, but also the shellfish species composition is changing, and probably is adapting itself to a new situation. What the role of fishermen is in steering this process is completely unclear so far.

8.2   Filling in the Normal Operation Range

Where ecosystem models e.g. predict the primary and secondary production, and the maximum amount of secondary producers in a system, they usually fail to predict what species might use the production space. For that part, a large number of descriptive and modelling tools is available.

8.2.1   Descriptive way to estimate species or functional group composition.

One important way of describing the ecosystem behaviour concerns the structuring of communities. Simple processes like predation or food availability may have different effect on animals depending on the position of the animals in a system. E.g. animals at the air/water boundary undergo a tidal emergence, and the relative emergence period and the accompanying food availability and predator pressure strongly structure the local community. This is well described for rocky tidal interfaces, but also valid for soft shore intertidal, like the Dutch Wadden Sea.
Beukema and Dekker (2005) described the influence of shrimp predation upon the apparent settlement characteristics of cockles (*Cerasteroderma edule*). In years with high standing stocks of shrimps early in the season, cockles spatfall mainly appeared in high intertidal areas, whereas the low intertidal was supposed to be the better environment for this shellfish species.

A nice example of the interaction between food, predation and species location was given by Hiddink (2004), who showed that just settled Baltic Tellin larvae (a medium sized bivalve) chose high intertidal sites, where predation pressure by shrimps was less than close to the low water line. Adult Baltic Tellins however, prefer a site close to the low water line, where food availability is better. During its life, the young shellfish show a migration pattern from the high intertidal regions down to the low intertidal. The balance between extra mortality (a consequence of the migration) and profit of a better environment in the low intertidal obviously is positive.

Saier (2001) and Buschbaum (2001) described a similar process on the structuring of intertidal and subtidal mussel beds in the Sylt-Romo-area (Germany). Where subtidal mussel beds have the best sites regarding food availability (algae filtered from the water column), they also undergo strong predation pressure by snails, small starfish, shrimps in the beginning of their life span, and larger starfish, crabs and eider ducks later on. They described that predation by juvenile starfish and crabs on barnacle epibionts caused a clean-up of mussel shells, resulting in lesser attachment area for new settling larvae. In the intertidal, the mentioned invertebrates are heavily predated themselves by birds, and there shellfish predation mainly is a matter of the occurring birds, like oystercatchers and gulls. During submersion, the subtidal predators may take over the process partly, but they have to escape the predation during emersion, and thus, they are restricted to the areas not too far from the low-water line.

Such processes can be described, and used for predicting effects of certain changes, e.g. an increase of shrimps due to whatever cause. But the variability is that high that a quantitative prediction is rather risky.

8.2.1.1 Varying nutrient supply

Sommer (1993) performed a lot of interesting microcosm experiments. He showed that the outcome of growth competition between a number of algae species not only depended on the amount of light or nutrients, but also on the frequency of nutrient addition. An alternating addition resulted in another community structure than a constant addition did.

8.2.1.2 Interspecific behaviour

Many types of interspecific relations exist:
- species may compete for food
  - indirect: feeding on the same source like filter feeding macrobenthos does, or algae growing on nutrients or competing for light,
  - more direct competition like the gull that eats the starfish or the kleptoparasitic behaviour of skuas against gulls, or gulls against eider ducks),
- species may compete for space: the already mentioned rocky shore assemblages are the best example, probably.

8.3 Quantitative estimates of how the normal operating range is filled, and associated processes.

Many types of models are developed with the aim to tell us about the way animals might be distributed in a known environment. The boundary conditions are assumed to be known; and this might concern the amount of food, or a total or maximum biomass, but also the suitability of an environment for a certain species to develop or to forage on the (again known) resources.

8.3.1 Habitat models

One relatively simple and at the same time arguable method is the one based on habitat modelling. The present occurrence of organisms is related to environmental characteristics. The relationship may be quantitative (some sort of a regression equation) to qualitative (a PCA). Many techniques have been developed to analyse such relationships. The method gives relatively fast results, but the relationships mostly are not necessarily causal. For predictions of the systems behaviour under changed environmental conditions, the method is not very reliable. The results might be useful for management since they give an idea of what might be expected and in what direction an response is to be expected, but the quantification of the effects is not very reliable.

8.3.2 Species specific behaviour

There are many studies on the behaviour of species. This concerns the functional response of species to e.g. food availability, salinity, temperature, oxygen conditions, etc. In some cases, intraspecific competition is quantified. An example of the last is the study on oystercatchers. Several researchers studied to feeding properties combined with the way birds react to other neighbour birds (see Van der Meer, 1997 for an overview). The derived functional responses allow us to quantify the utilisation of food available on tidal flats, and provide useful information for nature management and shellfishery policy. Another example is the work by Goss-Custard (1996) on Oystercatcher condition as affected by food availability and presence of foraging areas.

8.3.3 Positive feedbacks

An interesting mechanism concerns the effects that an organism (community of) may have is that it may positively affects the environmental conditions for its own presence. One example was illustrated by Brinkman & Smaal (2003) with an ecosystem model computation. They computed that in a tidal system, mussels (Blue Mussel, *Mytilus edulis*) as an important filter feeding species stores organic matter in the soft bottom sediments. As a result, the year-after-year accumulation of organic matter helps the system productivity through the sediment/water release of

nutrients. The breakdown of organic matter (partly) takes place during the critical periods of nutrient depletion. Without such a storage, secondary production will be considerably lower than with storage. This difference may be 25-50%, although these numbers are not very precise.

8.3.4 Multiple steady states

The possibility of multiple stable states is mentioned in many cases. A mandatory condition is that each stable situation is able to prevent (to a certain level) the transition into another stable situation. Numerically spoken: the stable states are not really stable, but only locally. Transition into another state requires an equivalent of the chemical activation energy: the state has to be pushed into another (or: the next) stable state. One nice example is described by Van Nes et al (in Amaro, 2005) and Amaro et al (2005) on the occurrence of brittle stars (*Amphiura filiformes*) and a burrowing shrimp (*Calianassa subterranean*). Both species seem to prefer different sediment characteristics (in terms of erodability: brittle stars prefer the more stable sediments). At the same site the shrimps replaced the brittle stars, and as these shrimps were able to maintain the higher erodibility of the sediments they prevented the return of the brittle stars.

The seagrass meadow story is another example of multiple stable states. At least in fresh waters, submerged water plants disappeared due to competition for light with pelagic and epiphytic algae in a highly eutrophicated environment. Fish communities that relied on the existence of plants as refuge, for example, disappeared and as a result, the community structure of the aquatic environment changed; favouring more pelagic algae and thus producing even less favourable conditions for submerged water plants. Only after strong reduction of nutrient inputs, partly combined with man-induced removal of bream as a zooplankton eaten fish, submerged water plants were able to return.

8.3.5 Expert systems

There are more possibilities to estimate system or species responses quantitatively. A few methods are situated a bit between descriptive and quantitative ones. Expert systems as a collection of knowledge and rules are exponents of organised descriptive estimates of system behaviour. The more complete the system, the more results of case studies will be part of such expert systems, ad thus, the change of containing answers to management related questions increases. As a major draw-back it might be considered that expert systems need experience based knowledge.

9 Dune- and forest ecosystems

Loek Kuiters

9.1 Multiple stable states

For the predictability of ecosystem development, and for restoration management of degraded dune and forest ecosystems in particular, the concept that many ecosystems may exist in multiple stable states, is relevant for setting restoration goals (Hobbs & Norton 1996). From the community ecology perspective, the ecological concept of multiple stable states (Lewontin 1969, Holling 1973) predicts that ecological systems may exist potentially in different stable states under similar environmental and climatic conditions (Beisner et al. 2003, Schröder et al. 2005)[1].

If multiple stable states exist for a particular ecosystem, then this has consequences for its conservation management. Unexpected and unpredictable outcomes of restoration efforts of degraded systems are often due to the focus on re-establishing historical disturbance regimes and/or abiotic conditions and subsequent successional processes, whilst ignoring changes in biotic factors and the feedback between biotic and abiotic factors (Suding et al. 2004; Kuiters et al. 2005). These feedbacks can make a degraded system resistant to restorative change (Bakker & Berendse 1999). One of the consequences is that successful restoration or development of certain successional stages (ecological or historical references) is not very realistic. At least it will need much more effort than simply restoring abiotic conditions. System thresholds and feedbacks should be incorporated to the dynamics of restoration of degraded systems (Suding et al. 2004).

Multiple stable state models can be used to predict when a system might gradually or rather suddenly collapse to a degraded state, as the result of gradual changes in climate, human exploitation of resources, atmospheric deposition, habitat loss or fragmentation. The dynamics of the degraded state are often very different from those in the pristine state. Restoration efforts might need to manipulate more than a single factor or process that led to the gradual degradation or more sudden collapse. There is an increasing amount of evidence that shows that degraded systems are resilient to ecological restoration management, which can be explained by assuming that these systems represent alternative states (Suding et al. 2004; Kuiters et al. 2005). Ecological constraints that create internal feedbacks should be identified. Ultimately, alternative management goals should be formulated offering room for new assemblages of species, based on changed abiotic, biotic and environmental conditions.

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[1] There are two different contexts in which the term *alternative stable states* is used in literature (Beisner et al. 2003, Mayer & Rietkerk 2004). Ecosystem ecologists use the 'ecosystem perspective' to indicate the potential for several different community types after a disturbance. (see May 1977, Scheffer et al. 2001). Population and community ecologists use the 'community perspective' to describe the possibility of the existence of different stable configurations of sets of coexisting species, under the same environmental conditions (Beisner et al. 2003)

Wilson & Agnew (1992) mention four possible outcomes of positive-feedback switches: a) occurrence of a stable vegetation mosaic in a previously uniform environment, 2) intensification of a vegetation gradient leading to sharp boundaries, 3) delay or 4) acceleration of succession by displacement or sharpening of temporal boundaries. Another outcome might be that coexistence is not possible and therefore intermediate states are lacking in the field.

Hereafter a few examples are worked out of studies which show in more detail the mechanisms that may produce multiple stable states in terrestrial ecosystems. Examples come from a) wet dune slacks, b) dry coastal dune grasslands, c) riverine dune grasslands, and d) grazed grasslands and tidal flats.

9.1.1 Wet dune slacks

Adema et al. (2002) found evidence that different successional stages may exist alongside each other within a dune slack. In an unmanaged part of a wet dune slack on Texel (De Muy), a pioneer stage of *Samolo-Littorelletum* dominated by *Littorella uniflora* coexisted for more than 60 yr together with a late successional stage of *Scirpo-Phragmitetum,* dominated by *Phragmites australis.* Neither the substrate nor the hydrological conditions differed between the two stages. Biotic interactions possibly explained the differences in vegetation development. As possible feedback-mechanisms, stabilising the pioneer stage, they mentioned:

a) Adaptation of pioneer species to anoxic and nutrient-poor conditions. A pioneer species such as *L. uniflora* shows radial oxygen loss which in a calcareous soil facilitates the rapid decomposition of organic matter. Nitrification may occur on a very local scale, with further away from the roots denitrification and thus nutrient losses (coupled nitrification-denitrification). Pioneer species are capable of facilitating decomposition of their own litter, or otherwise keep nutrient accumulation at a low level by stimulating nutrient losses from the system. Thereby they efficiently stabilise the pioneer phase (Adema et al. (2005).

b) Microbial mats often cover the soil surface in open pioneer vegetation. The activities of different functional groups of cyanobacteria, sulphur bacteria, and sulphate-reducing bacteria result in steep environmental micro-gradients of oxygen and sulphide in particular. Sulphide is toxic for most plant species. However, some dune slack pioneer species can protect themselves against toxic sulphide by releasing oxygen from their roots. This results in a stable pioneer vegetation which can not be invaded by later species.

c) Later successional species are more efficient in retaining nutrients in organic material and retrieve them the next growth season, so the internal nutrient cycle increases.

    One of the practical consequences they mention is that dune slacks that have entirely shifted towards a more productive state due to a disturbance will not simply return to a stable pioneer stage again when the disturbing agent is removed. Examples of disturbances are extraction of ground water and atmospheric nitrogen deposition. Management activities that focus on adjusting the competitive balance between early and late successional species, by mowing for instance, are tackling the symptoms of a change of ecosystem properties of

dune slacks. It will require a continued management effort and is therefore not very effective. Improving the conditions for ecosystem processes, such as restoring the hydrological regime or reducing the nitrogen input, that stabilises early successional stages with high species diversity, is more successful. Additional measures are necessary to restore the desired early-successional stage. For instance, sod-cutting might be applied to restore the abiotic conditions that are suitable for pioneer vegetation.

9.1.2   Coastal dune grasslands

Coastal dune grasslands have over the last few decades at many locations changed from open, species-rich systems to vegetation dominated by several coarse grasses. There is increasing evidence that dry dune grasslands may exhibit multiple stable states related to fertilisation and acidification processes. In the calcareous dunes of the *Renodunaal district*, characterised by a lime- and iron-rich sand substrate, the availability of phosphorus (P) and nitrogen (N) is naturally low. P is fixed in calcium phosphates and N-availability is low due to a low input of litter and a high microbial N-demand. Acid atmospheric deposition has in many parts resulted in an increased availability of P, whereas concurrently high N-deposition increased N-availability (Kooijman et al. 1998, Kooijman & Besse 2002). Resulting from this, biomass production has increased and a few productive monocotyledonous species, e.g. *Calamagrostis epigejos* and *Carex arenaria*, now dominate species-poor vegetation. By a positive feedback-loop internal soil acidification has increased due to a higher litter input and increased root exudation of hydrogen ions, which has further enlarged P and N availability. This again favoured high-productive competitive species, at the expense of less-competitive characteristic dune grassland species. The strong reduction of rabbit density in the 1950s due to myxomatosis, and in the 1990s as a result of the VHS-virus epidemic, has contributed to the further spread of dominant grasses. Restoration management such as introducing grazing ungulate herbivores are often not very successful and indicate that degradation stages are more or less resilient.

In the calcium- and iron-poor *Wadden district*, P remains available despite the low pH (Kooijman et al. 1998). The low iron and aluminium contents prevent P-fixation at low pH, and P is relatively loosely bound. N and P-availability are higher compared to the Renodunaal district. The vegetation is N-limited and sensitive to N-deposition. Nitrogen enrichment enables the expansion of a highly unpalatable and dominant grass-species *Ammophila arenaria*. It produces litter which is slowly mineralised (Veen & Kooiman, 1997). Contemporary, the species is very effective in re-translocation of nutrients from senescing tissue.

It is likely that grass-dominated dune grasslands are resilient to change as the result of a better competition for light and nutrients (Veen & Kooijman 1997). The nitrogen mineralization and availability is higher in grass-dominated dune vegetation. A positive feedback between grass-dominated vegetation and N-cycling enhances

grass encroachment. Due to high above-ground biomass interception of dry nitrogen deposition is higher. Additionally, rabbits do not forage on coarse grasses.

9.1.3 Riverine sandy dune grasslands

In the temporarily flooded areas of river banks, dry nutrient-poor grasslands with a high nature conservation value (*Medicagini-Avenetum*, *Festuco-Thymetum*) can be found on alkaline sandy soils with active buffering of calcium. They are part of a landscape mosaic characterised by pastures, heathlands and shrub communities. These landscapes were traditionally extensively grazed by cattle, and were affected by fluvial processes. The species-rich pastures occur often in meander cut-offs of the main river. For their maintenance they are dependent of periodically active deposition of overbank sediments. They require flood events of short duration and flooding frequency of 2 to 3 times per year (Wolfert et al. 2002).

After deposition of overbank sediments, soil forming processes start and gradually change soil properties. Organic matter accumulates in the top-soil and results in a natural soil acidification. The periodical deposition of fresh river sediments guarantees the supply of calcium, thereby buffering the acidification process and resetting site conditions and vegetation succession of the pastures. Not only too rare but also too frequent flooding would lead to the decline of the species-rich, dry pastures. However, natural levee deposition rates decrease with levee age. Rehabilitation of the natural levee disturbance processes is necessary to increase the suitable area for the establishment of these species-rich dry riverine pastures. This can be organised by removing local protection structures. Another strategy is to rehabilitate natural fluvial landscape dynamics, in order to enable the formation of new natural levees once the older levees have reached their maximum height. The formation of new natural levees is favoured by the occurrence of meander cut-offs.

In terms of multiple stable state-theory we might say that the system is degraded and has shifted to a new state. It cannot be restored to the previous conditions solely by re-establishing natural flooding regimes. For a successful restoration, another management strategy is needed which disrupts feedbacks between vegetation and soil (humus accumulation and soil acidification) and addresses the constraints of the degraded system.

9.2 Herbivore-mediated positive-feedback switches

9.2.1 Temperate ecosystems

In grazed temperate grasslands much less is known about multiple stable states, although there are a few studies available which indicate that they might occur here as well. Transitions between different states may be driven by grazing pressures. Several studies have been published on the encroachment of woody species in temperate grasslands in the presence or absence of grazing pressure (Olff et al. 1999,

Kuiters & Slim 2003, Bakker et al. 2004). Closed woody vegetation form a resilient alternative ecosystem state, which will not return to a grassland stage without 'catastrophic events' such as wind-throw, fire or human intervention.

One of the possible mechanisms behind herbivore-mediated vegetation shifts might be the spreading in grazed systems of unpalatable species (native or exotic) with effects on ecosystem characteristics, such as nutrient turnover rates. Once these species have changed ecosystem processes, positive feedbacks may increase the resistance of the system to a change in its former state. It creates an internally re-enforced state that is very difficult to change. An example of this was found in Alpine grasslands (Güsewell et al. 2005). Here a positive feedback system was found on so called 'camp areas' which are grazed intensely and receive most herbivore excreta. Plant tissue was richer in nutrients (especially P), which stimulated soil microbes. This promoted more nutrient-demanding species such as *Festuca rubra*, *Agrostis capillaris* and *Poa annua*. On the extensively grazed pastures, a rather species-poor vegetation developed with the rather unpalatable tussock grass *Narduus stricta* as most dominant species. It produced litter of poor quality (high lignin content) which had a low decomposition rate, which slowed down mineralization processes in the soil.

Spatial heterogeneity is a typical feature of grazing. The grazing animals tend to graze on areas with nutritious vegetation cover, whereas they select particular landscape features for resting and ruminating. Spatial segregation of grazing and excretion may result in a considerable redistribution of nutrients within the landscape and creates at a long term a heterogeneous pattern of soil nutrient availability. In response to patterns in nutrient availability and differential grazing pressure, different types of vegetation may develop within heterogeneously used pastures. This in turn affects the behaviour of the herbivores in a way that tends to reinforce the existing patterns. This is called a herbivore-mediated positive-feedback system (Wilson & Agnew 1992).

Another example for plant-mediated change of soil conditions by herbivores is from tidal flats. Van der Wal et al. (2000) found that early successional species such as *Triglochin maritima* and *Puccinellia maritima* were able to delay succession on salt marshes by attracting herbivores. Enhanced grazing increases nutrient losses and prevents the accumulation of a large nutrient pool by litter. This creates conditions to which early successional species are well adapted. Late successional species on salt marshes such as *Elymus pungens* are avoided by herbivores. By producing large quantities of litter, these vegetations stimulate the build-up of nutrients in the system.

9.3   Temperate forest systems

There is a large body of literature demonstrating the effects of ungulates on forest regeneration (Weisberg & Bugmann 2003, Côté et al. 2004). Especially deer species can inhibit the natural regeneration of particular tree species (Gill 1992, Kuiters & Slim 2002, Rooney & Waller 2003). Moreover, effects of herbivores on forest systems may be amplified by positive feedbacks between plant litter and soil nutrient availability, by changing forest canopy composition (Pastor et al. 1993, Hobbs 1996). Ungulate-browsing can favour browse-tolerant tree species, whose leaves often have

high lignin contents and high C/N ratio (Hobbs 1996), resulting in the long term in a slow-down of soil mineralization processes and litter accumulation. Ungulates thus might affect forest soil fertility.

Many studies have compared areas or sites with and without herbivores (e.g. exclosure-studies), but these only test the hypothesis that ungulates have a distinct impact on some aspects of forest dynamics. The question is, however, if large herbivores are able to drive or maintain forest systems in alternative stable states? There is some evidence that if fire or wind-throw drives tree densities in temperate forests locally to a low level, ungulates such as deer can then regulate tree regeneration and maintain the forest system in a grassland state, like elephants do in the Serengeti-Mara savannah woodlands in East Africa (Dublin et al. 1990). According the definition of multiple stable states, the system does not return to its previous state once the disturbing factor reverts to its previous level. Dublin et al. (1990) argued that there might be a new factor that takes over and holds the system in the new state. In the Serengeti savannah system elephants were not capable to seriously decline woodland cover and move the system to a grassland stage. But when tree cover was declined by a disturbance factor such as fire, they were able to ensure that the savannah stayed in the grassland stage by preventing woodland recovery. Reduction of fire frequency would prevent the system to return to the woodland stage.

Parallel to this we can state that prevention of tree regeneration by deer and other ungulates in temperate forests after wind-throw or (wild)fire may drive a forest system locally into an alternative stage composed of grasses, heathland and low shrubs (Kramer et al. 2003). For nature conservation purposes, a dynamic mosaic of alternative states of closed woodland vegetation and open grassland vegetation maintained by natural processes such as wind-throw, fire and herbivory is wanted. Therefore, it is very important to have more insight under what conditions such a mosaic can be developed and maintained. Most of our forests are static mono-species, even-aged stands, due to human exploitation in the recent and further past. The re-establishment of natural disturbance regimes and processes may enhance species-diversity. Opening up closed canopies by creating gaps of sufficiently size may accelerate this. For restoration management we need experiments with combinations of gap-sizes and manipulated ungulate densities, to find out how co-occurring alternative states can be re-installed.

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