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Biodiversity and Species Extinctions in Model Food Webs

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To Thomas, Julia & Lina

Abstract

Many of the earth's ecosystems are experiencing large species losses due to human impacts such as habitat destruction and fragmentation, climate change, species invasions, pollution, and overfishing. Due to the complex interactions between species in food webs the extinction of one species could lead to a cascade of further extinctions and hence cause dramatic changes in species composition and ecosystem processes. The complexity of ecological systems makes it difficult to study them empirically. The systems often consist of large species numbers with lots of interactions between species. Investigating ecological communities within a theoretical approach, using mathematical models and computer simulations, is an alternative or a complement to experimental studies. This thesis is a collection of theoretical studies. We use model food webs in order to explore how biodiversity (species number) affects the response of communities to species loss (*Paper I-III*) and to environmental variability (*Paper IV*).

In paper I and II we investigate the risk of secondary extinctions following deletion of one species. It is shown that resistance against additional species extinctions increases with redundancy (number of species per functional group) (*Paper I*) in the absence of competition between basal species but decreases with redundancy in the presence of competition between basal species (*Paper II*). It is further shown that food webs with low redundancy run the risk of losing a greater proportion of species following a species deletion in a deterministic environment but when demographic stochasticity is included the benefits of redundancy are largely lost (*Paper II*). This finding implies that in the construction of nature reserves the advantages of redundancy for conservation of communities may be lost if the reserves are small in size. Additionally, food webs show higher risks of further extinctions after the loss of basal species and herbivores than after the loss of top predators (*Paper I and II*).

Secondary extinctions caused by a primary extinction and mediated through direct and indirect effects, are likely to occur with a time delay since the manifestation of indirect effects can take long time to appear. In paper III we show that the loss of a top predator leads to a significantly earlier onset of secondary extinctions in model communities than does the loss of a species from other trophic levels. If local secondary extinctions occur early they are less likely to be balanced by immigration of species from local communities nearby implying that secondary extinctions caused by the loss of top predators are less likely to be balanced by dispersal than secondary extinctions caused by the loss of other species. As top predators are vulnerable to human-induced disturbances on ecosystems in the first place, our results suggest that conservation of top predators should be a priority. Moreover, in most cases time to secondary extinction is shown to increase with species richness indicating the decay of ecological communities to be slower in species-rich than in species-poor communities.

Apart from the human-induced disturbances that often force species towards extinction the environment is also, to a smaller or larger extent, varying over time in a natural way. Such environmental stochasticity influences the dynamics of populations. In paper IV we compare the responses of food webs of different sizes to environmental stochasticity. Species-rich webs are found to be more sensitive to environmental stochasticity. Particularly, species-rich webs lose a greater proportion of species than species-poor webs and they also begin losing species faster than species-poor webs. However, once one species is lost time to final extinction is longer in species-rich webs than in species-poor webs. We also find that the results differ depending on whether species respond similarly to environmental fluctuations or whether their responses are uncorrelated. For a given species richness, communities with uncorrelated species responses run a considerable higher risk of losing a fixed proportion of species compared with communities with correlated species responses.

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List of papers

The following papers are included in the thesis. They are referred to in the text by their roman numerals.

- I. Borrvall, C., Ebenman, B. & Jonsson, T. (2000). Biodiversity lessens the risk of cascading extinction in model food webs. *Ecology Letters*, 3, 131-136.
- II. Ebenman, B., Law, R. & Borrvall, C. (2004). Community viability analysis: the response of ecological communities to species loss. *Ecology*, 85, 2591-2600.
- III. Borrvall, C. & Ebenman, B. (2006). Early onset of secondary extinctions in ecological communities following the loss of top predators. *Ecology Letters*, 9, 435-442.
- IV. Borrvall, C., & Ebenman, B. (2006). Biodiversity and persistence of ecological communities in a stochastic environment. *Manuscript*.

Contribution to the papers:

Charlotte Borrvall contributed equally with co-authors in shaping the ideas, choice of methodological tools and formulation of the questions, in all papers. CB developed computer codes and made the analyses of the data and results for paper I, III and IV, and participated in the development of codes and in the data analyses of paper II. CB made a major contribution in the writing of papers I, III and IV and participated in the writing of paper II.

Introduction

Many of the earth's ecosystems are experiencing large species losses due to human impacts such as habitat destruction and fragmentation, climate change, species invasions, pollution, and overfishing (Jackson et al. 2001; Myers & Worm 2003; Thomas et al. 2004a; Thomas et al. 2004b). An important question raised by these accelerated species extinction rates is the extent to which the loss of biodiversity matters. How will species losses affect the stability of the ecological communities and what will happen to the productivity and other functions of the ecosystems? What role does biodiversity play in providing sustainable ecological goods and services for human societies? These questions are not easy to answer due to the fact that ecological communities are very complex, having lots of species interacting with each others and the environment. The extinction of one species could for example lead to the break-down of mechanisms enabling coexistence (Fig. 1), resulting in a cascade of ecological effects (Paine 1966; Estes & Palmisano 1974; Schindler et al. 1997; Pace et al. 1999; Borrvall et al. 2000; Jackson et al. 2001; Dunne et al. 2002a; Ebenman et al. 2004; Koh et al. 2004; Ebenman & Jonsson 2005; Borrvall & Ebenman 2006; Terborgh et al. 2006). Although we know little about the effects of species loss we know for sure that the rapid alteration of biodiversity could lead to unforeseeable consequences for the dynamics and functions of ecological communities (see Chapin et al. [2000] for a review). Predicting the response of ecological communities to species extinctions is therefore of greatest importance.

Apart from the human-induced environmental disturbances that often force species towards extinction the environment is, to a smaller or larger extent, varying over time in a natural way. These variations are also kinds of disturbances that influence the dynamics of populations. Anthropogenic disturbances often resemble lasting press perturbations while ordinary environmental variation can be compared with temporary pulses (Bender et al. 1984) that affect the populations now and then and results in fluctuating population densities (Strong 1986). Community responses to perturbations are related to the type and size of the perturbation that they are exposed to.

The arrangement of species and links in ecological communities determines the structure of the communities. Because perturbations propagate through communities via species interactions knowledge of the structure of the community is important for understanding the effects of perturbations on communities. How will the structure of a community affect its response to different kinds of perturbations? Are communities with certain structures more vulnerable than others with different structures? Are for example species-rich communities more capable of buffering environmental variability than species-poor ones?

Different species do not face equal risks of going extinct (Tracy & George 1992; Vitousek et al. 1997; Pauly et al. 1998; Pereira et al. 2004) nor does the extinction of different species lead to equal effects on the ecosystem (Borrvall et al. 2000; Borrvall & Ebenman 2006). Identifying which species in which

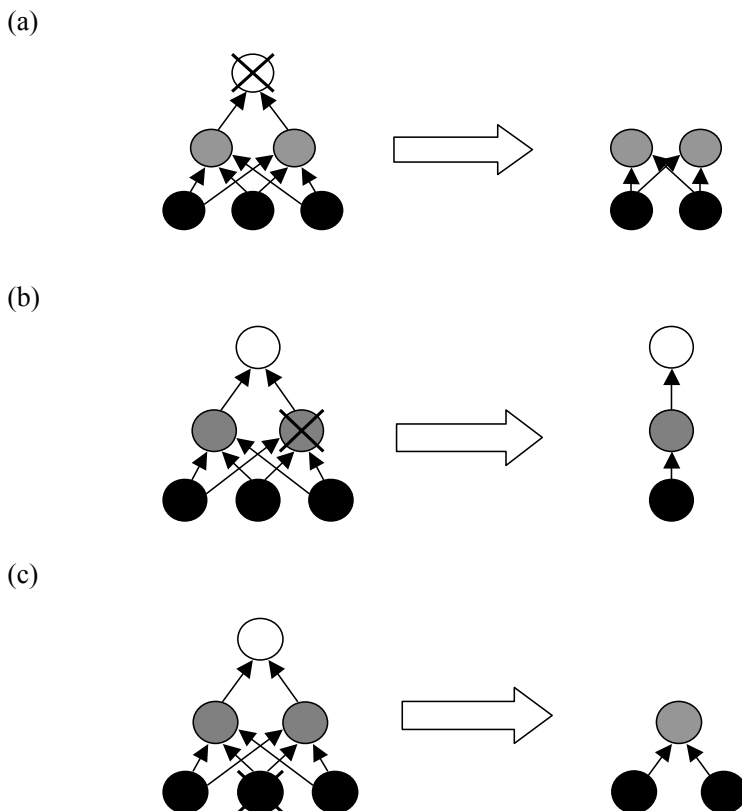


Figure 1. Mechanisms of secondary extinctions following the loss of one species (overcrossed circle). (a) Loss of a top predator leads to a top down extinction cascade. (b) Loss of a primary consumer results in disruption of predator-mediated coexistence. (c) Loss of a primary producer triggers a bottom-up extinction cascade.

communities that are most prone to extinction as well as which species in which communities that result in the largest effects on the ecosystem if they go extinct are urgent tasks if we want to be able to provide guidelines for conservation priorities.

Studying the effects of species loss in ecosystems using natural communities is almost an impossible task mainly due to the difficulties in defining community boundaries and with respect to the time-scale. Species can have long generation times forcing studies to last for decades whereas we need the answers today. An alternative is to perform controlled experiments in the laboratory (microcosms), or to use theoretical models of ecological communities. All approaches have their pros and cons and no one should exclude the other, instead they should be used as complements. In the theoretical approach ecological communities are often modelled as food webs

illustrated as graphs with nodes and links telling who eats whom in the community.

By means of a theoretical approach this thesis deals with the response of food webs to a large perturbation, species loss (*Paper I-III*), and the response of food webs to demographic (*Paper II*) and environmental stochasticity (*Paper IV*). The effects of species extinction are compared for food webs with different numbers of species per functional group (see below) in order to study the relationship between biodiversity and stability, which is a long-standing and largely unsettled issue (see McCann [2000]). More diverse communities (here higher number of species per functional group) could be thought to be more stable than less diverse communities because the loss of a species could be compensated for by functionally equivalent species.

Our results show that resistance against secondary extinctions, following the loss of one species, increases (*Paper I*) or decreases (*Paper II*) with redundancy depending on whether competition among basal species is present or not. Further, in a deterministic environment species-rich communities have a larger fraction of species remaining in the post-extinction community compared with species-poor communities (*Paper II*). However, in the presence of demographic stochasticity the benefits of redundancy are largely cancelled out by the effect of reduced population sizes (as redundancy increases more species are packed into the same finite area and the population sizes are reduced). This finding implies that in the construction of nature reserves the advantages of redundancy for conservation of communities may be lost if the reserves are small in size.

Following deletion of one species we also find that time to secondary extinctions often increases with increasing species richness (*Paper III*). If species extinctions occur early they are less likely to be balanced by immigration of species from local communities nearby. In this respect species-rich communities might be more persistent than species poor ones.

The effects of species deletion (risk of secondary extinctions, number and fraction of secondary extinctions, time to secondary extinctions, the trophic belonging of the species going extinct) are here shown to be affected by which species that initially is lost from the community. In particular, secondary extinctions resulting from initial deletion of top predators occur much faster compared with extinctions following deletion of species from other trophic levels (*Paper III*). As top predators at the same time are particularly vulnerable to human-induced disturbances on ecosystems our results suggest that conservation of top predators should be a priority.

According to the results from paper IV species-rich communities are more seriously affected by environmental stochasticity than species-poor ones in that per species risk of extinction, within a given period of time, increases with increasing species richness. These results are in contrast to expectations that biodiversity could help communities to cope with environmental stochasticity as the addition of more species to a community could increase the probability of finding tolerant species. However, environmental stochasticity can be added

to models in many different ways and it would be interesting to do extended simulations on similar but slightly different models.

The structure of food webs

It is commonly accepted that long term persistence of ecological communities is related to the structure of the communities (Pimm 1991; McCann 2000; Solé & Montoya 2001). Due to the scarcity of high-quality data and the lack of unified methods for analyzing the relationship between community structure and persistence it is not clear what structures that lead to long-term persistence and which criteria that must be fulfilled for a community to persist in the long run. So, what do natural communities look like and why? What structures lead to long-term persistence? These questions are the motives behind the studies of the relationship between community structures and persistence (see McCann [2000], and Ebenman & Jonsson [2005] for reviews).

A community can be illustrated by a food web describing the feeding relations in the community. Food webs are often viewed as graphs consisting of nodes symbolizing the species in the community and links connecting predators with their prey (Fig. 2). A food web can also be represented as a predation

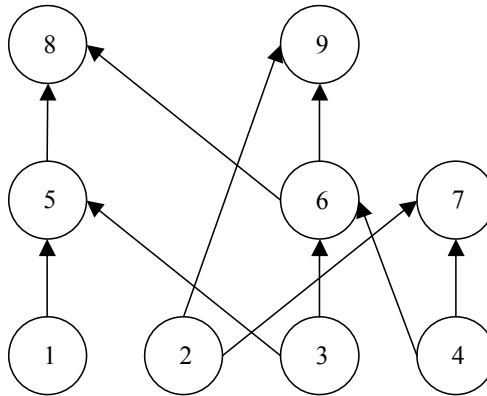


Figure 2. Graphical illustration of a food web consisting of 9 species.

matrix. This is a quadratic matrix with the element α_{ij} equal to 1 if species j predaes on species i , (i.e., if there is a link between species j and species i in the graphical illustration) and 0 otherwise (Fig. 3).

There are a few hundred described empirical food webs (Cohen et al. 1990; Schoenly et al. 1991; see references in Dunne et al. [2002b]) and many

ecologists have been and are involved in the search for patterns in these webs, i.e., attributes common to the food webs. The goal is to find out how food webs are structured and what factors being responsible for those eventual common

$$\begin{pmatrix} 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 1 \\ 0 & 0 & 0 & 0 & 1 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 1 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \end{pmatrix}$$

Figure 3. Predation matrix corresponding to the food web in figure 2. The matrix element α_{ij} is 1 if species j predates on species i (i.e., if there is a link between species j and species i in the graphical illustration in figure 2), and 0 otherwise.

features. However, most of the published webs are of poor quality why it is difficult to obtain general patterns.

Several structural properties of ecological communities can affect their response to species loss. In all papers in this thesis we have focused on *species number* in order to explore mainly the impact of species richness on the stability of food webs. We further touch upon different community geometries as well as different distributions of interaction strengths (*Paper I*).

Redundancy

Although conservation strategies have the objective to minimize the decline in biodiversity it is impossible to save every single species. According to Walker (1992) the important thing is to focus on the relation between biodiversity and ecosystem function. The question is: are all species equally important to ecosystem functioning or is there some degree of redundancy incorporated in ecosystems? Redundancy in ecosystems is a debated issue in discussions concerning the relationship between biodiversity and ecosystem functioning. The basic idea in the redundancy concept is that species which share a niche are ecological equivalents and that “species can be classified into guilds on the basis of their ecological function, including their effect on the environment and on other species” (Gitay et al. 1996). At one extreme, all species are believed to be unique and play important roles for ecosystem functions (see review in Johnson et al. [1996]). If one species is lost the function of the system is believed to change. If all species are important and have a constant effect on ecosystem function the relationship between species number and ecosystem function is linear. This hypothesis is called the

diversity-stability hypothesis (MacArthur 1955). At the other extreme, most species are thought to be redundant and the loss of those species is not believed to change the function of the ecosystem. This is the redundancy hypothesis (Walker 1992). The rivet hypothesis (Ehrlich & Ehrlich 1981) lies somewhere in between the two extremes. According to this point of view, some species can be lost without any greater effects on the community. When some threshold number has been reached, one additional species removal will cause the ecosystem to collapse (Johnson et al. 1996).

Redundancy can be said to provide insurance (Chapin et al. 1992; Walker 1992; Naeem 1998; Yachi & Loreau 1999; Thébault & Loreau 2005). Although species may be functionally redundant they may show *response diversity* (Elmqvist et al. 2003): they respond differently to environmental perturbations. Thus, following a perturbation some species in a functional group may go extinct meanwhile others may cope with the changed conditions, thereby sustaining the functionality of the community. In paper IV we add environmental stochasticity to food web models in order to investigate the relationship between biodiversity (species number) and vulnerability to environmental stochasticity. We use two different species response scenarios: (1) species responses to environmental stochasticity are correlated, and (2) species responses are uncorrelated.

In paper I-III we deal with *structural* redundancy, measured as the number of species per functional group. We define species to be structurally redundant if they share the same predators and prey (see Fig. 4). Although structural redundancy is different from functional redundancy discussed above, the two measurements should often be related. In paper I-III we explore how degree of redundancy in model food webs affects the response to species deletion.

Species types

Three main types of species can be distinguished in food webs. Those are basal species (species with no prey), intermediate species (species with both predators and prey) and top predators (species with no predators) (Fig. 4). If species are lost from communities it is reasonable to believe that the effects of extinction on the rest of the species depend on which species that is lost. Although species extinction sometimes can have dramatic effects on the rest of the community (Paine 1966; Estes & Palmisano 1974) this is not always the case. Paine (1969) introduced the keystone species concept which initially was applied to a predator in a rocky intertidal community. Experimental removal of the top predator resulted in greatly decreased species diversity. Since the introduction of the keystone species concept the term has been used frequently and it has been applied to species in different trophic levels and also in many different situations where the species in question has a major effect on community composition (see Mills et al. [1993]; Power et al. 1996). In paper I-III we use food webs with three functional groups: basal species, intermediate

species and top predators (Fig. 4). We investigate whether the effects of species loss depends on which species type that is deleted.

The fraction of species belonging to different trophic groups varies among different ecosystems. In this thesis we have studied two food web geometries: rectangular webs (equal number of species in the different trophic groups) and triangular webs (decreasing number of species with increasing trophic level) (Fig. 4).

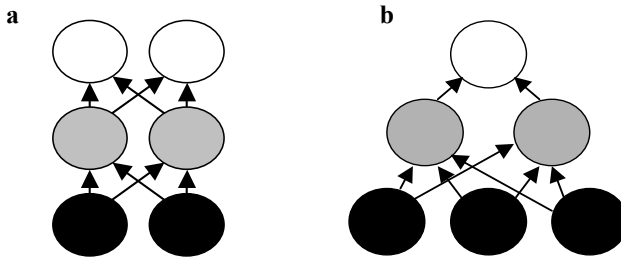


Figure 4. Rectangular (a) and triangular (b) food web with three trophic groups. Species belonging to the same trophic group are trophically equivalent, i.e., they share the same set of prey and predator species. Solid circles, basal species; grey circles, intermediate species (herbivores); open circles, top predators.

Interactions

Species affect each others by means of direct and/or indirect interactions. The patterning of interaction strengths (e.g., proportions of strong and weak links, different organizations of links) is suggested to affect the stability of food webs (May 1973; de Ruiter et al. 1995; Haydon 2000; Kokkoris et al. 2002; Neutel et al. 2002; Berlow et al. 2004; Emmerson & Yearsley 2004; Christianou & Ebenman 2005). It is not our intention to investigate this issue but we need to choose some distribution of the interactions in the food webs. Empirical estimates of interaction strengths (Paine 1992; Wootton 1997; Emmerson & Raffaelli 2004) suggest skewed distributions with mostly weak and only a few strong interactions. We therefore assume each predator to have a strong effect on one of its prey and weak effects on the others. In paper I we also investigate the case when a predator has equal effects on its prey species.

Theoretical analysis

The complexity of ecological systems makes it difficult to study them experimentally. The systems often consist of large species numbers with lots of interactions between species. Investigating ecological communities within a

theoretical approach, using mathematical models and computer simulations, is an alternative or a complement to experimental studies. During the last decades computer performance has increased drastically leading to amazing facilitation of calculations and simulations. As the high extinction rate we experience today hardly permits any long-term studies, theoretical studies are perhaps more relevant today than ever before.

Construction of food webs

Static models, such as the cascade model (Cohen & Newman 1985), the niche model (Williams & Martinez 2000) and the nested-hierarchy model (Cattin et al. 2004), have often been used in order to generate topologies of model communities. In these models links are not weighted, they are either present or non-present (meaning that the strengths of interactions between species are ignored). Another way of creating food web topology is the assembly process (Post & Pimm 1983; see Law [1999] for a review). This is a dynamic approach in which communities are built up by an iterative process. One species at a time is drawn at random from a species-pool and this species is tested to see whether it is able to invade the community or not.

The choice of approach in the construction of food webs will of course depend on the questions being posed. We create food webs instantaneously and because we want to study the role of species richness per se we keep large parts of the structure constant (e.g., connectance). We then parameterize the model webs by random draw of parameter values from some biologically reasonable predefined intervals ending up with a dynamic model.

Static or dynamic approach in detecting species extinctions

In order to reveal the consequences of species loss two approaches could be used: the static (Solé & Montoya 2001; Dunne et al. 2002a) and the dynamic approach (Pimm 1979; 1980; Borrvall et al. 2000; Ebenman et al. 2004; Borrvall & Ebenman 2006). An advantage with the static approach is that it makes no assumptions about the kinds of dynamics involved. Further, no data on interaction strengths or growth rates are needed. However, because the static approach does not deal with the dynamics of the species but consider only the link structure in the community this approach is able to detect only direct causes of species extinctions (consumers that lack resources). However, deterministic extinctions come about from both direct and indirect interactions among species. Clearly, a static approach is likely to underestimate numbers of secondary extinctions (Eklöf & Ebenman 2006). To be able to detect secondary extinctions that result from indirect effects we use a dynamic approach in the theoretical analyses of the communities. Such an approach takes into account the dynamics of the species thereby allowing both direct and indirect effects to be detected.

Dynamic models

Biological systems tend to be best described by sets of non-linear equations, and in studies of the dynamics and the persistence of communities the classical continuous-time non-linear model of Lotka and Volterra has often been used. In its original form, the model describes a predator-prey interaction, but it can be expanded to involve many species. In all papers we have used such a *system* of Lotka-Volterra equations to model food webs. In this system there is one equation for the growth rate of every species, i , in the system:

$$\frac{dN_i}{dt} = N_i \left(b_i + \sum_j a_{ij} N_j \right)$$

where N_i is the abundance of species i . For every species there are terms reflecting how this species' growth is affected by all the other species. There is no immigration or emigration. The per capita growth rates are linear functions of the densities of the species in the food web:

$$\frac{dN_i}{dt} \frac{1}{N_i} = b_i + \sum_j a_{ij} N_j$$

Here, b_i is the per capita growth rate of species i in the absence of intra- and inter-specific interactions. This parameter is positive if species i is a primary producer and negative if it is a consumer. The predators would thus die in the absence of prey. The terms a_{ij} denote the interaction strengths. This is the per capita effect of species j on the per capita growth of species i . If a_{ij} denotes a predator-prey interaction the term is positive if species j is a prey and i one of its predators, and negative if j is a predator and i one of its prey. a_{ij} could as well denote direct intra- (a_{ii}) or inter-specific competition.

The Lotka-Volterra model has been criticized for its simplicity, and its biological relevance has been questioned. Perhaps the most serious objection is the linear functional response of predators (Holling type I functional response) meaning that predators can consume an infinite number of prey items. Although linear functional responses might be appropriate descriptions in some ecological systems (e.g., when consumers have short handling times, or in low-productive environments) other kinds of consumption behavior might be more appropriate in others. Some recent studies use non-linear functional responses (see for example McCann & Hastings [1997]; McCann et al. [1998]; Brose et al. [2003]; Brose et al. [2005]). Here the per capita effect of a consumer on a prey is a function of the prey density, the handling time and the preference of the consumer (Holling type II functional response). Although species extinctions most often are attributed to some kind of stochastic variation, type II functional responses can produce long chaotic transients ending up in sudden

disappearances of populations, although no stochasticity is included in the model (McCann & Yodzis 1994). We use both type I and type II functional responses.

Once the choice of model is made one difficulty still remains: what values should the model parameters hold? Since predators have negative impact on their prey while resources have positive effects on their predators, the sign of the interaction strengths depends on which species is affecting which. Predators usually have larger impact on their prey than the reverse (except in donor-controlled systems), which should be reflected in the interaction strengths. Empirical studies suggest skew distributions of interaction strengths with mostly weak interactions (Paine 1992; Wootton 1997; Emmerson & Raffaelli 2004) and theoretical work suggest communities dominated by weak interactions to be more stable (May 1973; Kokkoris et al. 1999; McCann et al. 1998; Emmerson & Yearsly 2004). We use skew distributions of interaction strengths but we also compare results from simulations using skewed interactions with results from simulations using uniform distributions.

Since primary producers, when rare, are growing in abundance in the absence of predators, b_i is positive for those species. Predators will on the other hand starve if there is no prey, why b_i is negative for consumers. Animal predators are often larger than their animal prey, and a larger size leads to a longer generation time. Accordingly, intrinsic growth rates of the predators should be lower than the corresponding rates of the prey. The relative intrinsic growth rates of the primary producers will depend on the system. For example, in aquatic systems phytoplankton constitute the base of the food webs and they have higher intrinsic growth rates compared to trees that could be the ones making up the base of the food webs in terrestrial systems. Since the exact parameter values are not known they are often randomly drawn from intervals reflecting the magnitude differences discussed above. In our studies we have drawn the parameter values from uniform distributions.

It is not an easy task to choose the right model in theoretical work. On the one side you want the model to be a good descriptor of nature. On the other side you do not want the model to contain too many parameters as to complicate analyses and lose generality. We choose Lotka-Volterra models because it has been used for community descriptions for a long time and also because the Lotka-Volterra model is the only model that can be used to describe dynamics of communities with more than three species if the permanence criterion is to be used (*Paper II*). The use of bio-energetic models is another way of modeling community dynamics trying to incorporate some more biological realism into models (Yodzis & Innes 1992; McCann et al. 1998; Brose et al. 2005). Here, organisms are modeled as energy processors and the parameters involved are derived from empirical allometric scaling relationships. This means that physiological rates, such as respiration, can be estimated through body mass.

Criteria for persistence

In theoretical community stability analyses there is a need of a criterion for long-term persistence. Several difficulties are involved in the choice of the right criterion. It should of course reflect which communities being likely to occur in reality, but it also has to be mathematically tractable. Most of the theoretical work done in the past has been based on the assumption that the dynamics of natural communities can be described by deterministic models with stable equilibria (McCann 2000). The apprehension behind this is that communities with a stable equilibrium are more likely to be found in nature than are communities with an unstable equilibrium. Lately there has been a growing opinion advocating the use of nonequilibrium and stochastic models. This is because criteria based on equilibrium ignore dynamics not in the vicinity of equilibrium. In deterministic models species may be able to coexist on cyclic or chaotic orbits, although there is no stable equilibrium (Huston 1979; Huisman & Weissing 1999). Stochastic variation could lead to species extinction, but it could as well promote species coexistence by, for instance, preventing dominating species from outcompeting less dominant species (Chesson & Huntly 1997). Since communities are not intact forever but eventually loose species, one can also argue in favor of a criterion with the main interest of whether additional species are lost after the extinction of one species. This is a criterion of resistance.

Local and global stability

A biological system is said to be locally stable if it returns to equilibrium after small temporary perturbations in a deterministic environment (Lewontin 1969; May 1973; Yodzis 1989). Neighbourhood stability, asymptotic stability and Lyapunov stability are synonymous concepts (Lewontin 1969). The type of disturbance being connected to local stability involves temporary changes in population densities. The concept of local stability is built on the apprehension that locally stable communities are more likely to be found in nature than are locally unstable communities. The criterion is mathematically tractable and is therefore easy to use (May 1973).

In general, explicit solutions of a biological system of the form of the equation above can not be obtained. Instead, the solutions of the system (the vector of population abundances, N , as a function of time, t) can be seen as trajectories of N in the positive phase space of s dimensions where s is the number of species and the axes correspond to the species abundances (Yodzis 1989). Local stability analysis involves seeking for equilibrium points and investigating the dynamics around these equilibria. This can be done through linear approximation of the system. The community is termed locally stable if the real parts of all the eigenvalues of the Jacobian matrix are negative. (The elements of the Jacobian matrix are the partial derivatives of the function dN_j/dt , with respect to N_j , evaluated at the equilibrium.) In paper I we use the

method described above to check if the initial community is locally stable. We then delete a species from the community and check if the remaining community is locally stable, which implies that no further species has been lost. In paper III we use local stability analysis to create locally stable communities to give as start solutions at the numerical integration. As species could also coexist on cyclic or chaotic orbits one could argue that we might miss persistent states when we use the local stability criterion. However, in our studies (*Paper I, III*) all feasible communities are also locally stable meaning that we do not have any other dynamics. This is probably due to the presence of fairly strong intra-specific competition coefficients, and also to the absence of a saturating functional response.

In the concept of local stability, it is not clear *how* small a small perturbation is. The domain of the phase space from where the system will return to equilibrium is called *the domain of attraction* or *the basin of attraction* of the equilibrium (Yodzis 1989). If the system is locally stable, the deviation caused by a disturbance will die out and the system will return to equilibrium either as damped oscillations or monotonically. On the contrary, in an unstable system the deviation will grow leading either to extinction or reaching some other internal attractor.

When the dynamics of a set of species is studied, it is hard to draw a picture of the phase space if the number of species is greater than three. We can, however, still imagine a multi-dimensional phase space where each axis corresponds to one species' density. In this hyperspace one can differentiate between stationary states and transients (Lewontin 1969; Hastings 2004). In contrast to stationary states, transients are points where the system is on its way towards some attractor. A graphical view of the stationary states is to think of them as the flat areas in a patchy landscape, i.e., the hilltops and valley bottoms (May 1973). Whether a stationary state is locally stable depends on the landscape in the immediate neighborhood. A hilltop is for example always unstable since the smallest displacement will move the system to another point (May 1973). An attractor does not have to be a stable point but could as well be a stable cycle. This means that the species densities follow regular cycles.

The concept of local stability only gives information about what happens in the surroundings of a single point but tells us nothing about the behavior following large perturbations. This is clearly a drawback, because if the system is greatly perturbed it could collapse even though it is locally stable. On the contrary, if a system is globally stable it will return to equilibrium after every kind of disturbance, no matter how large it is. Imagine for example a crater of a volcano. The crater is a stable point, but if a disturbance is big enough the system will be carried out from the crater and move down the hillslope (May 1973). Accordingly, the volcano crater is a locally stable equilibrium but it is not a globally stable point. A global stability analysis gives information about the whole landscape, not only a single point. Because the system will return to a globally stable point from every other point in the phase space, it follows that if a point is globally stable there are no other stable points or cycles in the phase space (Lewontin 1969).

Is it possible to find more than one locally stable equilibrium point in a phase space, i.e., are there more than one possible community composition in a given habitat? If the equations describing the community dynamics are linear, local and global stability is identical, thus, there is only one locally stable equilibrium, where all the species are represented, which also is globally stable (Lewontin 1969). If the equations describing the community composition are non-linear there may exist multiple stable states where all species are present (May 1977). If there are multiple stable states, a locally stable point is not globally stable and slow and gradual changes in an environmental parameter can suddenly shift the system from one state to another (Scheffer & Carpenter 2003). Such drastic shifts could also be caused by basin boundary collisions (Vandermeer & Yodzis 1999).

Concentrating on asymptotic behavior, whether it is an equilibrium point, a cycle, or a chaotic dynamic, might be inappropriate if transients are long (Hastings 1996). The asymptotic states may differ a lot (in for example species composition) from the transient states. McCann and Yodzis (1994) have emphasized the importance of transients in the dynamics of food chains. They showed that long chaotic transients might precede sudden disappearances of populations.

Resilience

Suppose a system is frequently perturbed from its equilibrium. If the system is able to recover before it is disturbed again the system will spend most of its time near equilibrium. On the contrary, if the system is not able to recover between the disturbances it might be pushed further and further away from equilibrium, eventually leading to species extinction (Yodzis 1989).

Resilience (Pimm 1984) is the rate at which the species populations return to equilibrium after a temporary disturbance, and return time is the time it takes for the populations to return to equilibrium (Yodzis 1989). The concept of resilience/return time is related to the local stability criterion because there is no sense in measuring return rate and return time if there is no stable equilibrium (Stone et al. 1996; but see Ives [1995]). Of course, unstable populations do not return to equilibrium. In contrast to local stability, resilience and return time are *relative* measures of stability. This allows for comparisons of the degree of stability between different locally stable communities. Local stability is a qualitative measure which does not allow for such comparisons. Either is the system stable, or it is not.

Permanence

In the criteria of local and global stability the system is assumed to approach equilibrium. However, species might persist without tending towards equilibrium, for example, in a cyclic or chaotic manner. Hastings and Powell (1991) have for instance found chaotic behavior in a three-species food chain. Hence, the concepts of local and global stability may miss persistent non-equilibrium states. In addition, coexistence is not settled by the dynamics close to an equilibrium point but close to the boundary of the phase space where at least one species is rare. Some people argue that the important question for long term community persistence is whether all species in the system persist, i.e., the condition for persistence is that all species increase in abundance when rare. This is dealt with in the criterion of permanence (Hofbauer & Sigmund 1988; Anderson et al. 1992; Hutson & Schmitt 1992; Law & Blackford 1992; Law & Morton 1993; Law & Morton 1996; Morton et al. 1996; Morton & Law 1997; Jansen & Sigmund 1998), which is a stability concept dealing with the long-term coexistence of species in a community. A system is said to be permanent if all solutions that start in the positive phase space (all the densities N_i are positive) remain there (Anderson et al. 1992).

The criterion of permanence is global since all trajectories starting with positive species densities are included. Further, permanence places no restrictions on the kind of attractor. Instead, different types of dynamical behavior, for example, cyclic trajectories or chaotic states, are allowed (Anderson et al. 1992). Consequently, permanence does not reveal what the trajectories look like inside the phase space, it only states that the species are able to increase when rare and, hence, to coexist. Permanence is a qualitative concept in that it focuses on coexistence of species rather than on their abundances. For communities consisting of more than three species a check for permanence is only possible when the dynamics are described by Lotka-Volterra equations with linear consumer functional response.

As with the criteria of local and global stability, there are some disadvantages with the permanence criterion. First, a condition for permanence is that the boundary repels the solutions, resulting in positive species abundances. However, the solutions are allowed to pass very close to the boundary, meaning that the density of some species might reach very low values and therefore become sensitive to stochastic events (see below) and maybe go extinct. The restriction of the method to Lotka-Volterra dynamics is of course a serious limitation, but according to Peschel and Mende (1986) other dynamics can be transformed into Lotka-Volterra dynamics, indicating that this might not be such a serious problem after all. Third, the method described above may miss some persistent states. Since the concept of permanence is global, one solution tending to the boundary is enough for the system to be non-permanent. Thus, there might be local conditions where species are able to coexist although the system is non-permanent (Case 1995).

Resistance

One of the main criticisms of local stability is the small size of the perturbations that are allowed to influence the communities. Although the majority of the perturbations influencing ecological systems may be of a small size, the communities will sometimes be exposed to larger perturbations. Resistance is a stability criterion applicable in the case of small or large perturbations. The kind of perturbation involved is applicable in the case of permanent perturbations (compared with the transient perturbations present in the local or global stability analysis).

Pimm (1979) introduced *species deletion stability*, dealing with species loss. In essence, this is a criterion of resistance measuring the community's resistance against further species extinctions following the loss of a species. Since we right now are experiencing the sixth major extinction event in the history of life (Chapin et al. 1998), we are faced with questions making this criterion highly relevant. This is the main reason why we deal with the consequences of species loss in paper I-III.

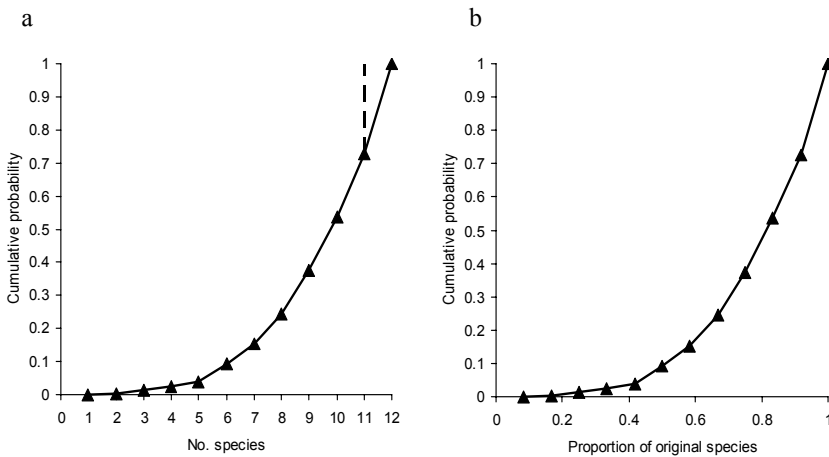


Figure 5. Risk curve for a 12-species community exposed to environmental fluctuations showing the probability that the post-extinction community are left with less than or equal to (a) a certain number of species or (b) a certain fraction of the original species number. The length of the vertical dashed line shows the resistance against extinctions.

In paper I and II we deal with resistance against further species extinctions following the deletion of one species. Resistance is here measured as the probability of no further species extinctions (*Paper I*) or as the probability of losing a certain number or fraction of species (*Paper II*). We deal with resistance also in paper IV, although here we do not delete a species. Instead we measure resistance against species loss in communities exposed to

environmental fluctuations. Resistance can be illustrated with the use of risk curves (Fig. 5).

Time lags and extinction debts

Although many species are doomed to go extinct following environmental changes such as habitat loss, there is often a time delay before species responses are visible (Wilcox 1978; Newmark 1987; Tilman et al. 1994; Brooks et al. 1999; Cowlshaw 1999; Berglund & Jonsson 2005; Vellend et al. 2006). In particular, when habitat changes are fast it can take a long time before the new species composition corresponding to the current structure of the landscape is reached. When species survival conditions no longer are met, there is only a matter of time before they will inevitably go extinct, they are “extinction debts” (Tilman et al. 1994). The time elapsed from habitat destruction until the new community composition is settled (all doomed species have gone extinct), is often referred to as *relaxation time*. Only a few studies have tried to estimate relaxation times, suggesting them to be in the order of 100 to 1000 years (Diamond 1972; Brooks et al. 1999; Vellend et al. 2006). However, as relaxation times are likely to depend on many factors such as size of habitat area, distances between fragments and dispersal abilities of the species, it is difficult to make comparisons between different studies. These kinds of species extinction occur as a result of altered survival conditions due to changes in the environment and interactions between species are not taken into account.

Secondary extinctions caused by a primary extinct species and mediated through direct or indirect effects, are also likely to occur with a time delay since indirect effects can take long time to appear (Yodzis 1988; Brown et al. 2001). The size of time delays might have important implications for the response of ecological communities to species loss. In metacommunities local extinctions might be balanced by dispersal of species between local communities (Leibold et al. 2004). If time delays are long there should be a greater chance of local extinctions being balanced by dispersal. An additional reason why it is important to pay attention to time lags is because this means that many species extant today are faced with impending extinction even where habitat loss now has ceased.

By means of numerical integration we study relaxation times of decaying food webs in paper III. More precisely we disturb communities by removing a species and we then follow the trajectories of the remaining species in the community. This enables us to record secondary species extinctions resulting from the loss of the first species. Relaxation time is measured as the time elapsed from the disturbance (initial species loss) until secondary extinctions take place.

Stochasticity

The stability concepts described above are all based on a deterministic environment. However, species live in stochastic (unpredictably variable) environments meaning that all populations in reality are influenced by uncertainty or random perturbations. Because stochasticity can have large effects on the dynamics and persistence of populations (May 1973; Roughgarden 1975; Lande 1993; Ludwig 1996), sometimes forcing populations towards extinction despite positive growth rates, excluding stochasticity from models could lead to underestimations of species extinctions. Environmental stochasticity (May 1973) refers to a randomly changing environment forcing population parameters to vary in an unpredictable manner. As a result, population dynamics are affected and might for example correlate with climatic variabilities (Grenfell et al. 1998) or show sustained oscillations (which would decay away in a deterministic environment) (Greenman & Benton 2003). Apart from environmental stochasticity populations are affected by demographic stochasticity (e.g. May 1973), having nothing to do with the environment but instead referring to the intrinsic uncertainty associated with the fate of each single individual in the population. Demographic stochasticity is likely unimportant in large populations, but may play an essential role and lead to extinction in small populations. Demographic stochasticity may eventually become important when population abundances have been suppressed to low levels due to environmental stochasticity.

One might often think of stochasticity as something that is harmful. It could for example lead to lowered competitive tolerance, resulting in species extinction (Chesson & Huntly 1997). However, stochastic variation could also have positive effects. Temporal fluctuations in environmental variables may keep species abundances at low levels, preventing dominating competitors from out competing less dominant species (Huston 1979). Spatial heterogeneity is another mechanism that may increase the probability of persistence (Levin 1974; Morrison & Barbosa 1987). Consequently, species may be able to coexist in a stochastic environment although they are unable to do so in a deterministic environment.

Although the approach for incorporating environmental stochasticity into community models have been available for quite a long time (May 1973) most studies dealing with community coexistence do not include environmental stochasticity. The trend has only recently started to change (e.g., Ives & Jansen 1998; Anderies & Beisner 2000; Ives et al. 2003; Sabo 2005; Brassil 2006).

Most studies dealing with the response of communities to environmental variation are done on one-species or two-species models (Cohen 1995; Ripa et al. 1998; Sabo 2005). The response to environmental stochasticity does not, however, depend on only the direct effects of the perturbation on the individual species' growth rates but also on the indirect effects acting through changes in the abundances of the other species in the community (Sabo 2005). It is therefore important to study the effect of environmental stochasticity on species extinctions in a community context.

Can biodiversity help communities to cope with a fluctuating environment? If different species with similar functions respond differently to environmental perturbations (*response diversity*, Elmqvist et al. 2003) theory predicts that the variability in community properties (such as total biomass) should decline with increasing species richness meaning that biodiversity provides insurance against environmental changes (Ives et al. 1999; Yachi & Loreau 1999; Ives et al. 2000). Adding more species to a community increases the probability of finding tolerant species and larger communities could therefore be able to cope with disturbances in a better way than smaller webs.

Earlier theoretical studies of the relationship between biodiversity (species richness) and community variability in fluctuating environments suggest that temporal variability in aggregate community properties, such as community biomass, should often decrease with species richness (May 1974; Doak et al. 1998; Hughes & Roughgarden 1998; Tilman et al. 1998; Ives et al. 1999, 2000; Tilman 1999; Yachi & Loreau 1999; Hughes & Roughgarden 2000; Lehman & Tilman 2000; Ives & Hughes 2002; Thébault & Loreau 2005). These studies have investigated the variation in species and community biomass for persisting communities, rather than having explored how environmental fluctuations might change the composition of a community. Their conclusions are therefore based on an assumption of low environmental variation. However, as environmental variation increases, the probability of species extinction increases (May 1973). It is therefore important to explore the risk and extent of extinctions in ecological communities subjected to a more highly variable environment. In paper IV we explore whether biodiversity (species richness) affects the response (risk of extinction and time to extinction) of communities exposed to environmental stochasticity. In contrast to the earlier studies mentioned above environmental stochasticity could here force species towards extinction, hence, we compare the degree of persistence of communities. There are several ways that the nature of stochasticity could influence the results but because not much is known about the nature of stochasticity in real communities we have tried to use simple assumptions about stochasticity. The choice of the point of entry of stochasticity is one thing that could affect the outcome. We chose to incorporate environmental stochasticity as direct perturbations to the species' per capita growth rates. The perturbations could also have been applied to, e.g., interaction strengths or abundances. The most appropriate point of entry is probably different for different types of perturbations. Another thing that is likely to influence the results is whether species respond similarly to perturbations (have a positive covariance), oppositely (have a negative covariance) or independently (the covariance is 0). In natural communities some species are likely to respond similar and others differently or independently. This will also probably depend on the type of disturbance. We have used two scenarios: either the species respond equally or they respond independently. Third, we have assumed environmental stochasticity to be totally uncorrelated over time. In natural communities it is likely that at least some kinds of perturbations are correlated over time in one way or the other.

Complexity and stability

The relationship between biological complexity and stability has a long and controversial history and many ecologists have been and are taking part in the debate (see Tilman [1999]; McCann [2000]), using different measures of both complexity and stability. Complexity has most often been measured as species number or connectance. Stability has been measured in many different ways. Different meanings of complexity and stability have contributed to the differences in the results concerning the relationship between them (Pimm 1984).

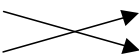
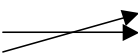
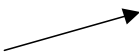
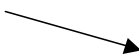
MacArthur (1955) was one of the first ecologists to relate community structure to stability. He used the number of energy paths (number of links in the food web) as a measure of complexity and argued that a community is stable if species abundances stay fairly constant over time. The hypothesis was that stability should increase (densities should vary less) with increasing number of energy paths in the food web, i.e., with increasing complexity. Elton (1958) and Odum (1953) were proponents of MacArthur, observing greater stability with greater complexity. These ideas became universally accepted although they lacked a strong theoretical and empirical foundation. In the early 1970s ecologists turned to mathematical models of food webs to explore the relationship between complexity and stability. They used the local stability criterion and most of these studies came up with similar conclusions: stability was found to decrease with complexity (Gardner & Ashby 1970; May 1972, 1973; Daniels & Mackay 1974). Also, resilience of model food webs was shown to decrease with complexity (Pimm & Lawton 1977; Pimm 1982). These new results seriously challenged the ideas from the 1950s and despite many limitations of these studies the paradigm was changed. However, the theoretical studies were largely criticized due to the limitations. Among the most serious critique was the use of randomly constructed food webs. These random webs contain biologically unrealistic structures (Lawlor 1978). When food webs were made more biologically plausible the result could be altered (Roberts 1974; DeAngelis 1975; Yodzis 1981). Other limitations of the theoretical work from the 1970s and 1980s are that they focus on one type of stability, local stability, which is only applicable in the near vicinity of an equilibrium point. Further, a number of phenomena characterizing ecological systems (such as environmental variability, ability for the system to adapt to changes etc.) are not included.

In summary, most theoretical studies show decreasing stability with increasing complexity (May 1972; Pimm & Lawton 1977; Chen & Cohen 2001; but see McCann et al. [1998]). This is a kind of paradox since real ecological communities often support large numbers of species. However, as May (1981) points out, "This is not to say that, in nature, complex ecosystems need appear less stable than simple ones. A complex system in an environment characterized by a low level of random fluctuation and a simple system in an environment characterized by a high level of random fluctuation can well be equally likely to persist, each having the dynamical stability properties

appropriate to its environment...In brief, a predictable ('stable') environment may permit a relatively complex and delicately balanced ecosystem to exist; an unpredictable ('unstable') environment is more likely to demand a structurally simple, robust ecosystem.”

The importance of community structures for the stability of ecological communities is now realized (DeAngelis 1975; Pimm & Lawton 1977; Yodzis 1981; Pimm 1984; McCann et al. 1998; Chen & Cohen 2001; Kokkoris et al. 2002; Brose et al. 2003; Kondoh 2003) and ecologists are presently investigating the impact of many different aspects of structure (e.g., compartmentalization, degree of omnivory, foraging adaptation) on community stability (Neutel et al. 2002; Kondoh 2003; Krause et al. 2003; Teng & McCann 2004).

Table 1. A summation of the four measures of stability that has been used in the papers of the thesis.

	<i>Measure of stability</i>			
	Resistance	Fraction of species lost	Time to sec. extinction	Per species extinction risk
<i>Effect of species increase</i>	Increases or decreases	Decreases or remains unchanged	Increases	Increases
<i>Cause of contrast</i>	Inter-specific competition	Demographic stochasticity		
<i>Complexity-stability trend</i>				
<i>Treated in Paper</i>	I, II	II	III, IV	IV

All papers in this thesis deal with the relationship between diversity (species number) and stability (different measures of stability in different papers). Partly depending on the measure of stability the thesis shows results in both directions (stability increases or decreases with increasing species number) (Table 1). Papers I and II show contrasting results concerning resistance against further species extinctions following the loss of one species. Resistance increases with species number when basal species lack inter-specific competition (stability increases) but decreases with species number when inter-specific competition is added (stability decreases). In a deterministic environment we show that

species rich communities lose a smaller fraction of species following deletion of one species (stability increases) (*Paper II*). This benefit of species rich webs is largely lost in the presence of demographic stochasticity (no stability trend). The time to secondary extinction following deletion of one species (*Paper III*), as well as time to final extinction following stochastic primary species extinction (*Paper IV*), increases with species number (stability increases). Finally it is shown that per species extinction risk is larger in species rich webs than in species poor ones (stability decreases) in stochastic environments (*Paper IV*).

Summary and future work

By means of a theoretical approach this thesis deals with the relationship between biodiversity (species number) and stability in ecological communities. The main contribution can be stated as follows:

- In a constant environment species-rich communities are more stable than species-poor ones in that they lose a smaller fraction of their species, following species deletion. This benefit of species richness is largely lost when demographic or environmental stochasticity is taken into account.

For the future, the following research topics are interesting continuations of the work presented in this thesis:

- To extend the work on stochasticity in paper IV, e.g., include temporal correlation in environmental variation, and assume different species response ranges in communities of different sizes.
- Include a spatial dimension, i.e., include species interactions on a spatial scale, in the framework of metacommunities.
- Include the possibility of consumer adaptation and the possibility of modifications of interaction strengths.

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