

Linköping studies in Science and Technology
Dissertations, No 1291

Species extinctions in food webs – local and regional processes

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Linköping, December 2009

Eklöf, A. 2009. Species extinctions in food webs – local and regional processes. Doctoral thesis. Department of Physics, Chemistry and Biology, Division of Theory and Modelling, Linköping University, Linköping, Sweden.

ISBN 978-91-7393-480-0

ISSN 0345-7524

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Front cover: Drawings by Frida Lögdberg
Photo by Bo-Inge Andersson

Printed by LiU-Tryck
Linköping, Sweden 2009

Till Fanny & Tuva

Med en önskan om att ni får växa upp
i en värld full av liv ♥

SUMMARY

Loss of biodiversity is one of the most severe threats to the ecosystems of the world. The major causes behind the high population and species extinction rates are anthropogenic activities such as overharvesting of natural populations, pollution, climate change and destruction and fragmentation of natural habitats. There is an urgent need of understanding how these species losses affect the ecological structure and functioning of our ecosystems. Ecological communities exist in a landscape but the spatial aspects of community dynamics have until recently to large extent been ignored. However, the community's response to species losses is likely to depend on both the structure of the local community as well as its interactions with surrounding communities. Also the characteristics of the species going extinct do affect how the community can cope with species loss. The overall goal of the present work has been to investigate how both local and regional processes affect ecosystem stability, in the context of preserved biodiversity and maintained ecosystem functioning. The focus is particularly on how these processes effects ecosystem's response to species loss. To accomplish this goal I have formulated and analyzed mathematical models of ecological communities. We start by analyzing the local processes (*Paper I* and *II*) and continue by adding the regional processes (*Paper III, IV* and *V*).

In *Paper I* we analyze dynamical models of ecological communities of different complexity (connectance) to investigate how the structure of the communities affects their resistance to species loss. We also investigate how the resistance is affected by the characteristics, like trophic level and connectivity, of the initially lost species. We find that complex communities are more resistant to species loss than simple communities. The loss of species at low trophic levels and/or with high connectivity (many links to other species) triggers, on average, the highest number of secondary extinctions. We also investigate the structure of the post-extinction community. Moreover, we compare our dynamical analysis with results from topological analysis to evaluate the importance of incorporating dynamics when assessing the risk and extent of cascading extinctions.

The characteristics of a species, like its trophic position and connectivity (number of ingoing and outgoing trophic links) will affect the consequences of its loss as well as its own vulnerability to secondary extinction. In *Paper II* we characterize the species according to their trophic/ecological uniqueness, a new measure of species characteristic we develop in this paper. A species that has no prey or predators in common with any other species in the community

will have a high trophic uniqueness. Here we examine the effect of secondary extinctions on an ecological community's trophic diversity, the range of different trophic roles played by the species in a community. We find that secondary extinctions cause loss of trophic diversity greater than expected from chance. This occurs because more tropically unique species are more vulnerable to secondary extinctions.

In *Paper III, IV and V* we expand the analysis to also include the spatial dimension. *Paper III* is a book chapter discussing spatial aspects of food webs. In *Paper IV* we analyze how metacommunities (a set of local communities in the landscape connected by species dispersal) respond to species loss and how this response is affected by the structure of the local communities and the number of patches in the metacommunity. We find that the inclusion of space reduces the risk of global and local extinctions and that lowly connected communities are more sensitive to species loss.

In *Paper V* we investigate how the trophic structure of the local communities, the spatial structure of the landscape and the dispersal patterns of species affect the risk of local extinctions in the metacommunity. We find that the pattern of dispersal can have large effects on local diversity. Dispersal rate as well as dispersal distance are important: low dispersal rates and localized dispersal decrease the risk of local and global extinctions while high dispersal rates and global dispersal increase the risk. We also show that the structure of the local communities plays a significant role for the effects of dispersal on the dynamics of the metacommunity. The species that are most affected by the introduction of the spatial dimension are the top predators.

POPULÄRVETENSKAPLIG SAMMANFATTNING

Ett av det största och mest akuta miljöproblemen idag är förlust av biologisk mångfald. Den naturliga utdöendehastigheten har under det senaste århundradet mångdubblats på grund av mänsklig påverkan så som förstörelse av naturliga miljöer, överexploatering av populationer, klimatförändring, introduktion av främmande arter och utsläpp av gifter och andra ämnen. Följderna av dessa utdöenden är svåra att förutse men att de kan få förödande konsekvenser visar flera exempel där förlust av en enda art orsakat kaskad av utdöenden och förändrat hela det ekologiska systemets utseende och funktion.

Ekologiska samhällen är mycket komplicerade vilket gör det svårt att genom enbart empiriska undersökningar förstå vad som händer när arter dör ut. En näringsväv är en förenklad beskrivning av ett ekosystem som visar hur samhällets olika arter är sammankopplade med varandra det vill säga vem som äter vem. Genom att utveckla dynamiska modeller av dessa system blir det möjligt att undersöka möjliga följder av utdöenden innan de skett. Det kan ge oss chans att sätta in åtgärder innan det är för sent. I den här avhandlingen utformas och simuleras matematiska modeller av ekologiska system.

Det finns flera faktorer att ta hänsyn till när man arbetar med ekologiska system. Dels hur deras struktur ser ut men också hur olika lokala samhällen interagerar med varandra genom att arter sprider sig där emellan. Den här avhandlingen behandlar båda aspekterna och kopplar samman ekosystems lokala (arters interaktioner inom lokala samhällen) och regional dynamik (hur arter rör sig mellan lokala samhällen). Målet är att identifiera vilka ekosystem som är extra sårbara, vilkas förlust ger upphov till extra allvarliga konsekvenser om de förloras och vilka arter som löper störst risk att drabbas av följdutdöenden. Generellt visar resultaten att komplexa ekosystem tål artförluster bättre än enklare system. Arter på basnivå, det vill säga växter ger störst konsekvenser när de förloras jämfört med arter på högre trofinivå. Arter på högre trofinivå löper däremot större risk att dö ut sekundärt. Också arter som är trofiskt unika, det vill säga har en för ekosystemet unik uppsättning av födointeraktioner, löper hög risk att dö ut i kaskadutdöenden. När en rumslig dimension introduceras minskar risken för sekundära utdöenden och att arter har möjlighet att sprida sig mellan olika lokaler har alltså positiv effekt. Ju fler lokala habitat som finns desto lägre blir risken för kaskadutdöenden. Däremot kan spridning mellan olika habitat kan också innebära en risk för individerna, speciellt om de måste röra sig genom områden de inte är anpassade för. Då kan den rumsliga dimensionen istället öka risken för utdöenden. Också arters spridningsmönster har betydelse för hur de påverkas av den rumsliga strukturen i ett landskap.

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- I. Eklöf, A. & Ebenman, B. (2006). Species loss and secondary extinctions in simple and complex model communities. *Journal of Animal Ecology*, 75, 239-246.
- II. Petchey, O., Eklöf, A., Borrvall, C. & Ebenman, B. (2008). Trophically unique species are vulnerable to cascading extinctions. *The American Naturalist*, 171, 568-579.
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- IV. Eklöf A., Platts, P. & Ebenman, B. (2009). Cascading extinctions in spatially coupled food webs. *Manuscript*
- V. Eklöf A., Münger, P. & Ebenman, B. (2009). Effects of dispersal on local extinctions in multi-trophic metacommunities. *Manuscript*

Permission to reprint the published papers was kindly granted by British Ecological Society (Paper I), The University of Chicago Press (Paper II) and Elsevier Inc. (Paper III).

Anna Eklöf contributed equally with coauthors in shaping the ideas, choice of methodological tools and formulation of the questions in all papers. AE developed computer codes for Paper I, for Paper II, IV and V together with coauthors. AE made the analysis of the results for Paper I, IV and V, and part of the analysis in Paper II. AE made a major contribution in the writing of Papers I, IV and V and participated in the writing of Paper II and III.

Overview

A major challenge in ecology is forecasting the effects of species' extinctions, a pressing problem given current human impacts on ecosystems, such as overharvesting, pollution, introduction of alien species, climate change and destruction of natural habitat (Tilman & Lehman 2001; Ceballos & Ehrlich 2002; Thomas et al. 2004). Consequences of species losses, such as secondary extinctions, are difficult to forecast because species interact in a complex network of ecological relationships. Because of their mutual dependence, the loss of a single species can cascade in multiple co-extinctions that will drastically change an ecosystem's structure and thereby its function (Paine 1966; Estes & Palmisano 1974; Borrvall et al. 2000; Sole & Montoya 2001; Dunne et al. 2002a; Koh et al. 2004). Of major importance when studying disturbances in ecological communities is to understand which species and structures play key-roles and are of extra importance for maintaining ecological structure and functioning.

Species exist in a landscape and thereby species interactions take place in a spatial context. All species are not present at all places at all points in time. Emigration and immigration events are important for the stability, diversity and productivity of ecological communities (Amarasekare 2000; Amarasekare & Nisbet 2001; Kerr et al. 2002; Loreau et al. 2003; Economo & Keitt 2008; Venail et al. 2008). Also, the anthropogenic activities mentioned above have consequences at large spatial scales. There is an urgent need for combining food web dynamics with spatial dynamics in order to improve our knowledge about structure and functioning in ecological communities (Holt 2002) and forecast effects of perturbations such as species loss (Holyoak et al. 2005).

Most ecosystems are extremely complex networks where many species interact with each other and their non-biotic environment. Collecting all the necessary data for understanding and predicting the response of these complex systems to human-induced perturbations is probably an impossible task, or at

the least a task that would take an enormous time, time we do not have. Trying to simplify these systems and model those, in cooperation with empiricists producing high-quality data, might be the only way to achieve an understanding of the ecological processes involved, an understanding we hopefully can use to manage the ecosystems in a sustainable way. In this thesis, I take a modeling approach to investigate the response of ecological communities to species loss. The aim of this thesis can be divided into two parts: first, to identify keystone species, structures in the community of extra importance and fragile communities using dynamical food web models and second, to develop models for linking together local processes (food web dynamics) and regional processes (spatial dynamics) of complex ecological systems. The overall goal has been to investigate how these processes affect ecosystem stability, in the context of preserved biodiversity mainly after a species loss.

Local processes

Food webs as binary networks

To be able to construct good models of ecological communities, we need to know the organization of real communities. Studies of the topological structure of natural food webs may provide clues for understanding community organisation and its relationship to different types of stability (Pimm 1991; Warren 1994; McCann 2000; Allesina & Pascual 2008). Basic structural properties of food webs are the number of species (S), the number of actual links (L) and the connectance (C , defined as the number of links, L , divided by the maximum possible number of links, S^2). Recently ecologists have also been showing an increasing interest in using graph theory (see Strogatz 2001 for a review) to describe the structure of food webs and to explore their response to species loss (Sole & Montoya 2001; Dunne et al. 2002a; Dunne et al. 2002b; Montoya & Sole 2002). The studies have dealt with network properties like

degree distribution (the distribution of trophic links among species), clustering coefficient (the fraction of pairs of neighbors of a node that are also neighbors of each other) and characteristic path length (the average shortest path length between all pairs of nodes)(Dunne et al. 2002b; Montoya & Sole 2002). Many complex networks share some topological features, like the ‘small world’ behavior (Strogatz 2001) and sometimes also scale-free distribution of links. This means that most nodes have few connections while a few nodes are very highly connected. Small world networks with scale-free distributions of links are rather robust to random removal of nodes but show high fragility when the most connected nodes are selectively removed, which eventually leads to fragmentation of the network structure into small sub-webs (Albert et al. 2000). In ecological networks like food webs, nodes represent species and network links represent direct trophic interactions between species. Even though there are different opinions whether food webs display small world behavior and have scale-free distribution of links (Dunne *et al.* 2002b; Montoya & Sole 2002), topological analyses of food webs have shown that they are very vulnerable to selective removal of their most connected species (Sole & Montoya 2001; Dunne et al. 2002a). In *Papers I* and *II* we find similar trends using dynamical models (see the section about food webs as dynamical networks). However, there are studies indicating that food webs can be sensitive also to removal of species with few links and that highly connected species often have many redundant links (Allesina et al. 2009; Dunne & Williams 2009).

Other topological properties of food webs like the connectivity correlation (degree correlation) (Melián & Bascompte 2002a) and the compartmentalisation (modularity) of food webs (Krause *et al.* 2003; Teng & McCann 2004) have also gained attention. Connectivity correlation is the relation between the connectivity of a node (species) and the average connectivity of its neighbors. The presence of compartments in natural food webs and its possible effects on the stability of the webs has been highly debated (May 1972; Pimm 1979b).

Recent studies indicate that increased degree of modularity enhances stability (Krause et al. 2003; Teng & McCann 2004). However, except for the study by Krause et al. (2003), few studies have evaluated the effects of large perturbations like the loss of a species in this context.

Topological analyses of binary food webs can give some information about the robustness of food webs to species loss (Briand & Cohen 1987; Cohen et al. 1990; Martinez 1994; Sole & Montoya 2001; Dunne et al. 2002a; Dunne et al. 2002b; Montoya & Sole 2002; Allesina & Pascual 2008). However, a binary representation of species interactions is an extremely simplified picture of food webs. Neither the growth rates of species nor the strengths of interactions between species are taken into account. Therefore, effects of indirect interactions (see Box 1) among species will not be revealed using the topological approach (see Borer et al. 2002). Thus, a topological analysis of binary, static food webs might reveal little about the consequences of perturbations like species loss (Holt 1977; Paine 1980; Borer et al. 2002; Dunne et al. 2002a; Dunne et al. 2002b; Ebenman & Jonsson 2005, *Paper I*). The strength of direct interactions (both interspecific and intraspecific) as well as indirect interactions has been shown to have large impact on the dynamics and stability of ecological communities (Bender et al. 1984; Abrams 1987; Abrams 1992; Menge 1995; Abrams et al. 1996; Fox & Olsen 2000; Dill et al. 2003). We have therefore taken a dynamic approach to assess the risk of secondary extinctions following the loss of a species. In *Paper I* we also compare results obtained from dynamic analysis with those obtained from topological analysis. We find that topological analyses underestimate the effects of species loss, especially in complex systems.

Food webs as dynamical networks

The nature of species interactions

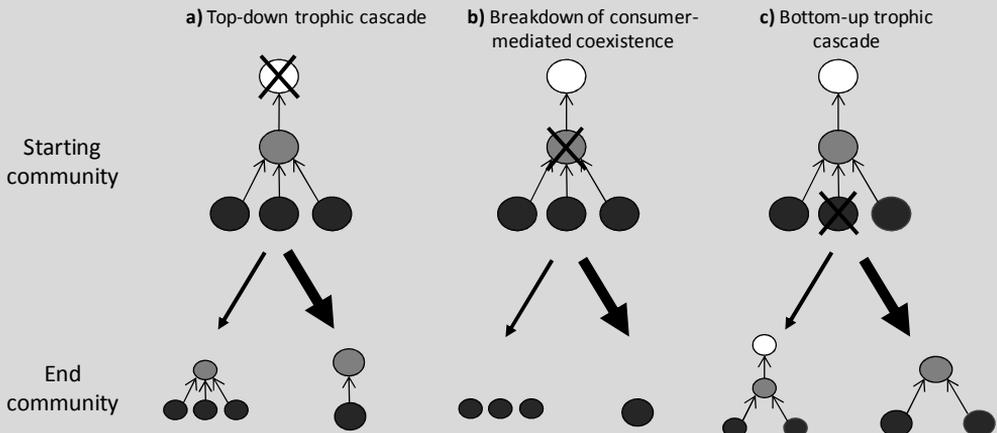
The main differences between topological and dynamical analyses of ecological communities is that in dynamical analysis the strength of the interactions between and within species is taken into account as well as species growth/mortality rates. Empirical studies suggest that interaction strengths are often highly variable (Berlow 1999; Berlow et al. 1999) and that their distributions are often skewed towards weaker interactions (Paine 1992; Fagan & Hurd 1994; De Ruiter et al. 1995; Raffaelli & Hall 1996). Several studies show that the patterning of interaction strengths in ecological communities has important effects both on the stability (McCann et al. 1998; Neutel et al. 2002; Emmerson & Raffaelli 2004; Christianou & Ebenman 2005; Maser et al. 2007; O'Gorman & Emmerson 2009, reviewed by Berlow et al. 2004) and functioning (Hulot et al. 2000; Duffy 2002) of the communities. Measuring interaction strengths in real ecological communities is a challenging task. However, it has recently been shown that the body size ratios of interacting organisms can be used to estimate interaction strengths (Emmerson & Raffaelli 2004). There are also suggestions that species-specific metabolic parameters, which also relate to species body size, can be used to estimate the strength of interactions (Yodzis & Innes 1992; Brose et al. 2006).

There are several ways to define interaction strengths (Berlow et al. 2004). In our analysis in *Papers I* and *II* we use the elements in the interaction matrix, which describe the direct effect of a single individual of one species, on the *per capita* growth rate of another species. More precisely, these are the interaction coefficients in the generalized Lotka-Volterra equations (see following section, Equation 1) when linear functional response of type I is assumed. In *Paper V* we have assumed functional response of type II.

In addition to the direct pair-wise interactions between species, like predation, competition and mutualism, there are also indirect interactions.

Indirect interactions are an important source of complexity in natural communities (Yodzis 1988; Wootton 1992; Wootton 1993; Menge 1995; Abrams et al. 1996). Examples of indirect interactions are trophic cascades, apparent competition, predator-mediated coexistence, exploitative competition and indirect mutualism (Wootton 1994; Morin 1999). Both direct and indirect interactions govern the response of ecological communities to perturbations like species loss (see Box 1). It is far from clear which of these interactions is most important. The presence of complex indirect interactions makes it more difficult to predict a community's response to a disturbance.

Box 1: Mechanisms of secondary extinctions



Mechanisms of secondary extinctions following species loss. The initially lost species is over-crossed in the picture. The thin arrow points at the end community if only food web topology have been taken into account. The thick arrows points at the end community where also population dynamics have been taken into account. **a)** Loss of a top predator causes top-down trophic cascade. **b)** Loss of an intermediate species causes break-down of consumer-mediated coexistence among the basal species. **c)** Loss of basal species triggering bottom-up trophic cascade. Modified from Ebenman and Jonsson (2005).

Lotka-Volterra model

Ecological systems are usually described by sets of non-linear equations, and in studies of the dynamics and the persistence of communities, the classical, continuous-time, Lotka-Volterra model has often been used. In *Papers I, II, IV* and *V* we have used such a system of Lotka-Volterra equations to model population dynamics in the food webs (in *Papers I, II* and *IV* with functional response type I, in *Paper V* type II). The generalized Lotka-Volterra equations have the following form

$$\frac{dx_i}{dt} = x_i \left(b_i + \sum_j \alpha_{ij} x_j \right) \quad (1)$$

where

x_i is the abundance of species i .

b_i is the *per capita* growth rate of species i in the absence of trophic interactions.

α_{ij} is the *per capita* effect of species j on the *per capita* growth rate of species i .

Lotka-Volterra models have been criticized for oversimplification of real community dynamics and their biological relevance has been questioned. Perhaps the most serious objection is the assumed linear functional response of predator consumption to prey density. The so called type I functional response (linear) assumes that a predator individual always consumes the same fraction of the prey population independent of prey density. In reality, this kind of functional response is probably only realistic in very few communities, where consumers have extremely short handling time or in very low-productive environments. Instead it might be more realistic to use a non-linear functional response. In the type II functional response the *per capita* effect of a consumer on its prey is a function of prey density, predator handling time, prey preference and attack rate. The predator consumption rate gradually approaches a maximum where it levels off.

We used linear (type I) functional response in *Papers I, II* and *IV*. That allowed us to use permanence as a stability criterion. Permanence is a stability criterion that ensures that all species densities stay strictly positive and increase when approaching zero (see section below). Testing for permanence in systems with more than three species is possible only for systems with linear functional responses for all consumers (Hofbauer & Sigmund 1988). In *Paper V* we used a saturated functional response (type II) and checked for feasibility (all species densities above predefined extinction thresholds) using numerical integration instead of using the permanence criteria.

There exist modifications of the Lotka-Volterra model, for example a consumer-resource model by Yodzis and Innes (Yodzis & Innes 1992) which has been extended to multispecies systems and developed to the Allometric-Trophic-Network (ATN) model (Brose et al. 2006; Berlow et al. 2009). Here the parameters are functions of species body mass, and the response variable is changes in relative biomass densities.

Criteria for community persistence

In order to investigate the response of ecological communities to different kinds of perturbations we need to have some kind of criteria for the long-term coexistence of interacting species. There are several stability criteria to choose among; the most commonly used being local asymptotic stability, global asymptotic stability and permanence.

Feasibility

Feasibility is a property all ecological systems shall have. In ecological terms, a feasible system is one that, in principle, can exist in nature, e.g. where all species have strictly positive densities. This means, for instance, that all consumers should have at least one prey.

Local and global asymptotic stability

The dynamical theory of food webs is to a large extent based on local stability analysis. A deterministic biological system is locally stable if all species densities return to the equilibrium point after a small temporary perturbation (May 1973). The relevance of local stability as a criterion for persistence of ecological communities has been questioned because it holds only in an arbitrarily small neighborhood of the equilibrium. Thus, it is only applicable in the case of 'small' perturbations. However, it is not clearly defined how small a 'small' perturbation has to be. Local stability does not guarantee the persistence of food webs affected by large perturbations. Moreover, complex dynamics such as periodic and chaotic attractors, which may be consistent with community persistence, are excluded (Hastings 1988; Law & Blackford 1992; Law & Morton 1993). Thus, global stability and permanence might be more appropriate criteria for community persistence.

Global stability means that the densities of species return to the equilibrium point after any temporary perturbation, no matter the size of the perturbation. Like the criterion of local stability, the global stability criterion for persistence is based on the existence of a stable equilibrium point. Thus, complex dynamics such as periodic and chaotic attractors that might be consistent with community persistence are excluded. It is usually very difficult to establish global stability for complex food webs (Pimm 1982).

Permanence

Local and global stability both assume that long-term persistence requires that a system is approaching some kind of equilibrium point. This means that non-equilibrium states are missed. The criterion of permanence, on the other hand, makes no assumptions about the dynamic behavior of the system; equilibrium behavior as well as more complex dynamic behavior is allowed. A community of n species is permanent if the boundary of the n -species phase space is a

repellor to orbits that start in the interior of the phase space (Hofbauer & Sigmund 1988; Law 1999). In other words, any trajectory that starts in the positive region of the phase space is repelled by all phase space boundaries. Permanence does not require the interior fixed point(s) to be locally or globally stable. This makes sense in an ecological context, since there is no reason to assume that the densities of coexisting species are always drawn toward some perfect balance.

In our analysis in *Papers I, II* and *IV* we have used permanence as the criterion for long-term persistence: firstly, to ensure that communities occupying an area can persist before a primary extinction takes place and secondly, to find the post-extinction community once the primary and secondary extinctions have taken place.

Numerical integration

There are situations where it is not possible to use the stability criteria mentioned above. An alternative is to follow the species dynamics over a certain time period, long enough for the system to settle, and check for persistence. We take this approach in parts of *Paper IV* and *Paper V*.

Measuring a community's response to perturbation

Keystone species and community viability analysis

There are different ways to look at an ecological community's response to perturbation. In this thesis (*Papers I, II, IV*) we deal with species loss, which is a severe and permanent perturbation that might trigger a cascade of secondary extinctions (Pimm 1979a; Pimm 1980; Borrvall et al. 2000; Sole & Montoya 2001; Dunne et al. 2002a). Secondary extinctions might have severe effects on the species composition and thereby the functioning of the community. It is therefore important to measure the risk and extent of secondary extinctions. Community viability analysis (Ebenman et al. 2004; Ebenman & Jonsson

2005) is a technique that can be used to accomplish this goal. It can be applied to identify keystone species, species vulnerable to secondary extinction and fragile community structures. Such information is crucial for effective conservation and management of ecosystems and natural resources. The technique is to construct a model of a community that reflects the structure of real ecological communities. Thereafter the community's response to species loss is investigated through numerical experiments. In earlier work, the probability that there will be no further extinctions following a species loss has been called *species deletion stability* (Pimm 1979a; Pimm 1980) or *resistance* (Borrvall et al. 2000). To quantify communities' responses to species loss in this thesis we use the *average number of secondary extinctions* (*Paper I*) and the *probability of cascading extinctions* (*Papers II and IV*). How the community is affected by species removal depends on the community's structure, the characteristics of removed species as well as the characteristics of secondarily extinct species.

Initial community structure

As discussed in sections above, the structure of ecological communities is of importance for how the community responds to perturbations, and particularly to species loss. The structural properties we have looked at in this thesis are connectance (*Papers I, II and IV*), distribution of interaction strengths (predators interacting with equal strength, with all their preys or having higher preference for one of its preys respectively, in *Papers I and II*) and food web shape (triangular or rectangular, e.g. more species at lower trophic levels or equal number of species at all trophic levels respectively, in *Paper I and II*). Particularly we found that communities with low connectance are especially vulnerable to species loss.

Characteristics of the removed species

How an ecological community responds to species loss depends on the characteristics of the initially lost species. This is important for stability, species composition and number of secondary extinctions (Dunne et al. 2002a; Christianou & Ebenman 2005, *Paper I*). Keystone species are species whose removal has relatively large effects on community diversity and composition (Paine 1969; Mills et al. 1993). Characteristics of a species that affect its keystone status are for example trophic level, connectivity and pattern of interaction strengths. Also the structure of the community where the species is embedded can be of importance (Mills et al. 1993; Borrvall et al. 2000; Christianou & Ebenman 2005, *Paper I*).

Both studies taking a topological and dynamical approach have found that removal of primary producers have on average more dramatic consequences compared to removal of consumer species. In addition, the studies also show that the keystone status is context dependent; the effects of removing a primary producer decrease with increased community diversity and connectance. The studies taking a dynamical approach have shown that removal of a top predator has more far reaching consequences in communities with high connectance compared to communities with low connectance (*Paper I*).

Characteristics of the secondary extinct species

Species have different functions in the community and some species may be more redundant than others. Identifying which species become secondarily extinct is therefore of major importance for the functioning of the post-extinction community. Also, here the characteristics of the species such as trophic position, connectivity and distributions of interaction strengths can determine its vulnerability. Intuitively, one might think that poorly connected species are most likely to suffer from secondary extinctions, as they have to

lose fewer links to stand without preys. While this is true in relatively sparsely connected communities, the opposite might be true in more complex ones. There, more highly connected species can suffer greater risk of secondary extinctions, possibly because they experience more indirect effects. These patterns have been observed in both microcosms (Fox & McGrady-Steed 2002) and theoretical studies (*Paper I*).

In *Paper II* we develop a new measure for describing trophic similarities and differences among species in a community - trophic uniqueness. Trophic uniqueness is related to how unique a species' niche is, in particular, how distant a species is from all other species in multidimensional niche space. The trophic uniqueness of a species will be low if it has many predators and preys in common with other species in the community, and high if it has few predators and preys in common with other species (Figure 1). If available, the strength of trophic interactions is also taken into account in the measure of trophic uniqueness. In *Paper II* we investigate both natural and model food webs and we find that trophically unique species are more likely to go secondarily extinct. The explanation for this is probably that intermediate species tend to become secondarily extinct more often and they also, on average, have a high trophic uniqueness. The mechanisms involved in the secondary extinctions of intermediate species are both direct bottom-up effects, due to the loss of their prey, and also top-down effects, due to disruption of predator-mediated coexistence when a top predator is deleted.

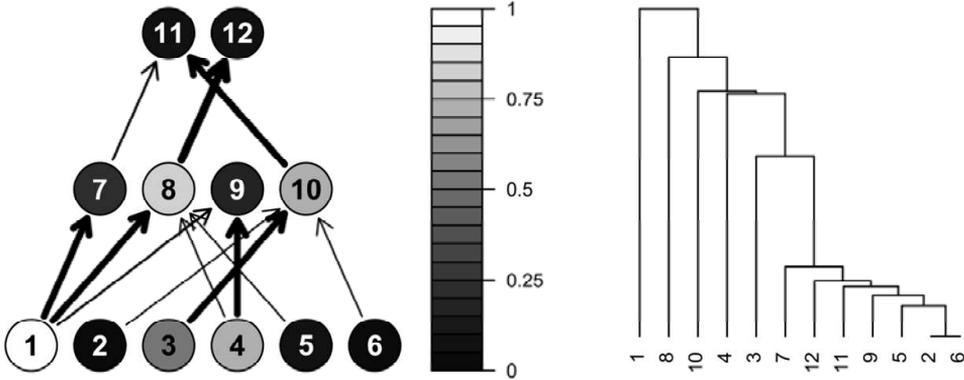


Figure 1. Graphic picture showing the feeding interactions in a food web. Thick arrows indicate a strong interaction and thin arrows indicate a weak interaction. Species with arrangement, number and strengths of feeding interactions very different from any other in the community are relatively unique in their trophic role (lighter shades of gray) and contribute with a proportionally large amount of trophic diversity in the entire community. In this example species 1 is very unique because it has two strong feeding links and a unique set of consumers. In contrast, species 2 and 6 have identical trophic roles; both are only consumed by species 10. In the dendrogram trophic diversity is the total branch length and a species trophic uniqueness is the length of its terminal branch. From *Paper II*.

Regional processes

Most often, representation of food webs is static, describing species and their interactions at a particular place and in a particular point of time. However, the structure of a food web may in reality vary both in time and space (Warren 1989, *Paper III*). Studies of ecological communities are traditionally concerned with investigating and explaining the patterns of species distribution, abundance and interactions. Such studies often ignore the fact that all ecological communities persist in a spatial arena and are open to varying amounts of immigration and emigration. On the other hand, studies of spatially distributed populations (metapopulations) have focused on how the

subpopulations interact with each other through dispersal of individuals, but interactions between species within the local patches have been ignored. In other words, while traditional studies on food webs and their dynamics have disregarded space, studies incorporating space have not taken species interactions into account. It is only recently that studies considering food webs of interacting species in a spatial setting have been performed (Melián & Bascompte 2002; Loreau et al. 2003; Brose et al. 2004; Koelle & Vandermeer 2005).

Natural, pristine habitats are more or less heterogeneous at all different scales of resolution from centimeters to kilometers. Knowledge of how species and populations will distribute themselves among different habitat patches is important for the understanding of observed spatial patterns. Moreover, such knowledge is of growing significance since natural ecological communities are increasingly being fragmented from larger continuous habitats into smaller partially isolated habitat patches (Sih et al. 2000; Fahrig 2003; Berlow et al. 2004; Holyoak et al. 2005). Habitat destruction and fragmentation is one of the most severe threats to the biodiversity in ecological communities today and these processes affect the spatial structure of communities in several ways. The number and size of patches as well as the distance between patches change which implies isolation and edge effects. The importance of connecting the local food web dynamics with regional spatial dynamics when investigating communities' responses to disturbances such as habitat fragmentation has been emphasized in recent studies (Melián & Bascompte 2002; Solé & Montoya 2006).

Melián and Bascompte (2002) showed that species' responses to habitat loss are not only determined by the spatial structure of the landscape (here number of habitat patches) but also by the structure of the food web in which the species are embedded. In other words, we need to have knowledge of how

species interact in space when the goal is management of ecosystem diversity and functioning.

Metacommunities

Ecological processes operating at other spatial scales than those typically addressed by population dynamic models, such as Lotka-Volterra equations and their extensions, have been recognized to be important (Wiens 1989; Holt 1993). Such processes include for example source-sink dynamics, mass effects and rescue effects (see Box 2), which involve interactions among local communities at larger scales. This is incorporated in the framework of metacommunities. A metacommunity is a set of local communities linked by dispersal of multiple potentially interacting species (Gilpin & Hanski 1991; Wilson 1992; Leibold et al. 2004; Holyoak et al. 2005). Dispersal can alter local species diversity both directly and indirectly through local community processes that feed back to alter features of the regional community (Leibold et al. 2004; Holyoak et al. 2005). In a review article, Leibold et al. (2004) divided research about metacommunities into four main approaches: patch-dynamic, species-sorting, mass-effect and neutral approach. The four approaches differ in how metacommunity characteristics are interpreted. The characteristics are mainly the relative timescale of local and regional processes (population dynamics and dispersal, respectively), species traits (competitive abilities, dispersal rate etc.) and patch quality (abiotic features equal or not). However, it has been shown that ecological communities usually do not fit into one single approach (Ellis et al. 2006). The approach we use in *Papers IV* and *V* does not fit to one of the approaches but is a combination of several; local and spatial processes occur on similar timescales and the patches differ in quality. Most important from this review is that the authors show that taking both local and regional scales into account leads to changes in the interpretation of ecological phenomena. In particular, source-sink dynamics in a metacommunity both

modifies local diversity as well as altering regional diversity (Donahue et al. 2003), e.g. local phenomena feed back on regional characteristics and vice versa.

Box 2: Metacommunities - Glossary

Patch	A discrete area of habitat
Population	All individuals of a single species in one patch
Metapopulation	A spatially structured single species population linked by dispersal
Local community	A set of species interacting with each other in a single habitat patch
Metacommunity	A set of local communities linked by dispersal of one or several species
Spatial dynamics	Any mechanism where species dispersal and distribution in space affect local and regional population dynamics

Mechanisms of spatial dynamics

Source-sink dynamics	Localities where species have declining densities without dispersal (sinks) are enhanced by immigration from other localities where populations increase without dispersal (source)
Mass effects	A net flow of individuals is created by differences in population densities in different patches
Rescue effects	Local extinction of species is prevented by immigration of individuals from other patches
Spatial coupling	Occurs when higher order consumers move over large parts of the metacommunity and thereby couple resources and their habitats in space

Spatial properties determine food web structure

One of the most widely observed patterns in ecology is the power-law scaling of diversity with habitat area. A recent study by Brose et al. (2004) combines this theory with the power-law scaling of trophic links between species in a community and species richness. Their model accurately predicts how trophic links scale with area and species richness of microcosms, lakes and streams from community to metacommunity level. This shows that spatial properties,

like habitat area, affect the trophic structure of ecological communities. It has also been shown by Holt (2002).

Soil-ecologists have argued that food webs are composed of fast and slow energy channels (Ruiter et al. 1995). A fast channel is a specific food chain in a larger food web where the turn-over rate (productivity:biomass ratio) is high, e.g. energy is transported quickly up through the trophic levels. Species interaction strengths can be derived from the turn-over rate between species, and fast energy channels will thereby correspond to food chains with strong interactions. The different channels have been shown to be separated in space across a wide range of ecosystems, for example pelagic (fast) and benthic (slow) channels in aquatic systems. The fast and slow energy channels (strong and weak interaction chains) are suggested to be coupled in space by organisms at high trophic levels when foraging in different channels at different points in time. This architecture has been detected in food webs across a range of ecosystems (Rooney et al. 2006). This implies that the spatial distributions of primary producers and predator movements are important for the structural organization of ecological communities (Rooney et al. 2006; Rooney et al. 2008).

Species movement in ecological communities

Different kinds of species movements affect a community in different ways. First, there are the foraging movements of species occurring when individuals are searching for food items in the landscape. This act of movement is based on species individual behavior and takes place on a faster time scale than the local food web dynamics (births, deaths, species interactions). Secondly, there is movement occurring more seldomly like natal dispersal, seasonal migrations and other emigration/immigration movements. These processes take place on a comparable or slower time scale than local food web dynamics. Foraging movement gives rise to spatial coupling of local food webs (McCann et al. 2005) whereas the dispersal acts on demographic processes and gives rise to

metacommunity dynamics (Leibold et al. 2004; Holyoak et al. 2005). Spatial coupling occurs when species at higher trophic levels are more mobile compared to their prey and tend to switch prey in time and space (McCann et al. 2005). The impact depends on predator scale of movement and resource distribution in space. Metacommunity dynamics occur via dispersal of one or several species between different local communities. While spatial coupling depends on the movement of higher-order consumers (since they usually move over larger areas, see for example McCann et al 2005), the metacommunity dynamics are affected by all species' movements. Dispersal that occurs on the same timescale as local dynamics directly influences species interactions, whereas dispersal that occurs on a longer timescale has no direct impact on species interactions but affects colonization/extinction dynamics.

Community boundaries

In nature, species interactions take place at many different spatial scales, from microsites holding one single individual to large regions of several square kilometers. Metacommunity theory simplifies this continuum of scales to two; local and regional scale. Even then, it is not completely clear in empirical situations how to divide metacommunities into those two spatial scales. The biggest problem is perhaps that local communities do not always have discrete boundaries; where is the actual boundary for a habitat? As rough approximation ecological communities can be divided into three categories; 1) discrete permanent habitat patches, 2) discrete temporary habitat patches and 3) patches with indistinct boundaries (Leibold et al. 2004). The first category is for example islands in the ocean where the characteristics of the surrounding area are completely different from the characteristics of the habitat patch and the boundaries are therefore very well defined. The second category is assemblages of habitat patches that from time to time have very well defined boundaries, for example water filled tree holes or intertidal water filled ponds.

The third category is probably the one including most of the habitats in nature. Here the boundary of the habitat patch is more gradually changing into the surrounding area, such as one type of vegetation changing to another type of vegetation. An additional difficulty, strongly coupled to the boundary problem, is that different species may respond to ecological processes at different scales. What one species experiences as a local patch, a different species may not experience in the same way. If these species also interact, directly or indirectly, there are several different spatial scales in one metacommunity.

Connectivity of the landscape

How dispersal affects local and regional dynamics and diversity in a metacommunity depends on the composition of local communities and the degree of connectivity between these localities (Kneitel & Miller 2003). The persistence of spatially structured populations depends to large extent on the connectivity of the landscape (Holyoak 2000a; Urban & Keitt 2001; Montoya et al. 2006; Solé & Montoya 2006; Bodin & Norberg 2007). Landscape connectivity can be described using graph theory (Strogatz 2001; Montoya et al. 2006; Bodin & Norberg 2007; Urban et al. 2009). Here the nodes represent habitat patches or local populations and links represent the functional connections, via species dispersal, among populations. Landscape connectivity and patch characteristics can be described by different network measures (see Strogatz 2001 for a review). However, the distribution of patches must always be put in the context of how the species of interest experience the landscape in order to understand the functional connection of local populations and communities. Species at different trophic levels often have different dispersal patterns in the landscape, where species at higher trophic levels tend to move over larger areas compared to species at lower trophic levels (McCann et al. 2005; Rooney et al. 2008, *Paper III*). This leads to species-specific differences in the experiences of patch connectivity. A basal species in a food web might be

restricted to only one specific patch or perhaps also the closest neighbor patches and experience the landscape as very fragmented, whereas a top predator in the same food web can move freely in the whole metacommunity and experience it as one continuous habitat. The landscape connectivity is then different for different species interacting in a food web and depends on both the number and distribution of local habitats as well as species dispersal patterns.

Of particular interest in conservation biology is the search for patches, or groups of patches, that more than others contribute to the traversability of the landscape (Bodin & Norberg 2007). This can for example be patches with high between centrality connecting different sub-groups of patches or important source patches that provide their neighbors with new individuals. Such key-patches are supposed to be of extra importance for the persistence of the metacommunity and there would be relatively large negative consequences if they were lost. However, because species experience the landscape differently, different patches might be key-patches to different species. To sum up, local food webs can be seen as networks and the landscape where they exist can be seen as another network. A metacommunity is thereby a complex entity of several interacting networks whose dynamics are dependent on each other.

Body-size dependent dispersal

Large species tend to be both larger and more mobile than small species (Peters 1983). The scale of movement and individual home range increases with increasing body size (Blueweiss et al. 1978; Peters 1983; Jetz et al. 2004; McCann et al. 2005). There is also a clear positive relationship between species' trophic level and body size (Cohen et al. 1993; Cohen et al. 2003; McCann et al. 2005; Rooney et al. 2008). Consumers at high trophic levels will therefore act like couplers and link together resources and their habitats in space (Rooney et al. 2008; McCann & Rooney 2009, *Paper III*). Also, larger organisms

tend to have bigger and more complex brains, and a larger brain would allow the consumer to more efficiently make foraging decisions in a wider range of habitats (Rooney et al. 2008). This permits predators to switch between prey populations and thereby release pressure when resource density is low and increase pressure when resource density is high. This mechanism will dampen fluctuations in lower trophic levels (McCann et al. 2005). This indicates that large animals, like top predators, have important contributions to ecosystem function and stability via spatial coupling of sub food webs. This is discussed in more detail in *Paper III*.

Dispersal as a promoter of stability

Species movements make recolonization and rescue effects possible. This is one of the reasons why dispersal can be positive for species persistence. However, these mechanisms can only operate if populations in different patches fluctuate asynchronously. If all local populations experience low densities simultaneously there will be an increase in risk of global extinction of that species, e.g. synchrony of population dynamics may be dangerous for species. Most studies of persistence of interacting species in a spatial context have been done on competing species at one trophic level, pairwise predator-prey interactions or small food web modules. I will give a short overview of the mechanisms involved in these kinds of studies.

Competing species

In metacommunity studies of competing species, the analysis is usually done on species that are not able to coexist without dispersal, e.g. one of the species (the superior competitor) constantly outcompetes the other species (the inferior competitor) in a closed community. In homogenous landscapes the same species is the superior competitor in all patches. Here the inferior competitor cannot maintain a positive growth rate in the absence of dispersal and is

excluded from the whole metacommunity. Classical theory suggests that coexistence is possible only when the inferior competitor is more mobile and thereby can invade local communities where the superior competitor is absent (Levins & Culver 1971). However, these ideas have been developed in later studies (see Amarasekare 2008b). In heterogeneous landscapes the species' competitive rankings can vary in space, e.g. a species is the superior competitor in some patches and the inferior competitor in other patches. The key to getting stabilized coexistence is in both cases inclusion of dispersal (Amarasekare & Nisbet 2001; Amarasekare 2003). Of major importance is that dispersal rate is sufficiently low since too high dispersal rate tends to synchronize localities and too low to prevent the release of competition pressure.

Pairwise predator-prey interactions

Fluctuating predator-prey interactions can be stabilized by the inclusion of habitat subdivision and dispersal (Holyoak & Lawler 1996a; Holyoak & Lawler 1996b). This can occur via three mechanisms (Briggs & Hoopes 2004; Amarasekare 2008b). The first mechanism arises in heterogeneous landscapes. Here, limited dispersal gives rise to asynchronous spatial dynamics as immigration becomes negative density dependent. This dampens the fluctuations in local communities and thereby dampens fluctuations in the metacommunity as whole, which increases metacommunity persistence. A requirement is that dispersal has to be sufficiently low to keep the asynchrony between patches.

The second mechanism arises in homogenous landscapes when the resource has limited dispersal and the consumer has global dispersal. The result is that resource density varies significantly between different localities. When the consumer has a non-linear functional response, this reduces the consumer efficiency and decreases the interaction strengths to the resource.

The third mechanism arises in homogenous landscapes when the consumer has limited dispersal. This enables the maintenance of consumer-resource dynamics that differs between localities. Even though the local dynamics are not stabilized, the densities in the whole metacommunity are more stable via the asynchrony between local patches. The key to get a stable coexistence is in all three mechanisms limited dispersal and thereby preserved asynchrony.

Stabilizing effects of habitat subdivision and species dispersal have been shown to have stabilizing effects of predator-prey interactions and enhance persistence (Holyoak & Lawler 1996a; Holyoak & Lawler 1996b; Holyoak 2000b; Holyoak 2000c). Also the degree of connectivity in the landscape and arrangement of patches is important for persistence of predator-prey interactions (Holyoak 2000a).

Simple food webs

In simple food webs the mechanisms are fairly similar to those in competing and pairwise consumer-resource interactions but more complex effects can arise due to indirect effects. The key to coexistence is, again, asynchronous dynamics and limited dispersal which increase both local community and metacommunity persistence. An additional finding when looking at modules with more species interacting is the existence of key-dispersers, species whose dispersal pattern has disproportionately large effects on metacommunity diversity and persistence (Amarasekare 2008b). Depending on the mobility of the different interacting species, different species may become key-dispersers (McCann et al. 2005; Amarasekare 2008a). For example, in a simple predation module (one basal, two intermediate and one top species) with metacommunity dynamics dispersal of the top predator has no effect when the inferior competitor is immobile but large effect when it is mobile. In food webs with spatial coupling the large bodied top predator is suggested to always play a key-role (Amarasekare 2008b).

Additional studies have shown that the consequences of migration depend on the details of the food web in which the population of interest is embedded (Koelle & Vandermeer 2005). Koelle and Vandermeer (2005) analyzed a metacommunity with two patches and a simple food chain (one species at each trophic level) in each patch. They found that decreased effective distance between patches (increased connectivity) gave a decrease in population synchrony. Here the decrease in effective distances is a result of either increased migration rate or increased survival rate of migrating individuals. This indicates that conservation efforts that lead to increased connectivity in the landscape (such as designing corridors or improving matrix) can make the populations more asynchronous and thereby increase population persistence. Studies on single-species systems show, however, contrary results (Earn et al. 2000). In multispecies systems a local population's degree of synchrony is affected by migration patterns not only of its own members but also by the migration patterns of the species with which it interacts, directly or indirectly. Increased migration does not always mean increased synchrony of the local population dynamics, but depends on which species is migrating, landscape connectivity and local web structure (Koelle & Vandermeer 2005).

Changes in effective distance can have complex effects on population synchrony, especially when different species have different sensitivities to changes in inter-patch connectivity. Those effects cannot be revealed from simple pair-wise interactions (but see Holyoak 2000a). This shows the importance of taking a food web approach when analyzing spatial systems.

General mechanisms

Analysis on ecological communities with spatial dynamics included often shows evidence of species dispersal as a positive factor for stability, diversity and productivity (Holyoak & Lawler 1996b; Amarasekare 2000; Holyoak 2000a; Amarasekare & Nisbet 2001; Kerr et al. 2002; Loreau et al. 2003; Economo &

Keitt 2008; Venail et al. 2008). However, it is often shown that the positive effects occur at an intermediate dispersal rate and often vanish when dispersal rate is high or low. An increased dispersal rate most often leads to increased level of synchronization between local populations (but see Koelle and Vandermeer 2005). This increases the risk of extinction of the entire metapopulation through generating a temporally correlated extinction event and precludes rescue effects (Blasius et al. 1999). However, synchronization can also lead to the emergence of complex chaotic dynamics that might be important for species persistence (Blasius et al. 1999). A decreased dispersal rate, on the other hand, makes local populations too isolated and exposed to extinction due to low migration rate between patches. This leads to a hump-shaped relationship between dispersal rate and metacommunity diversity (Figure 2).

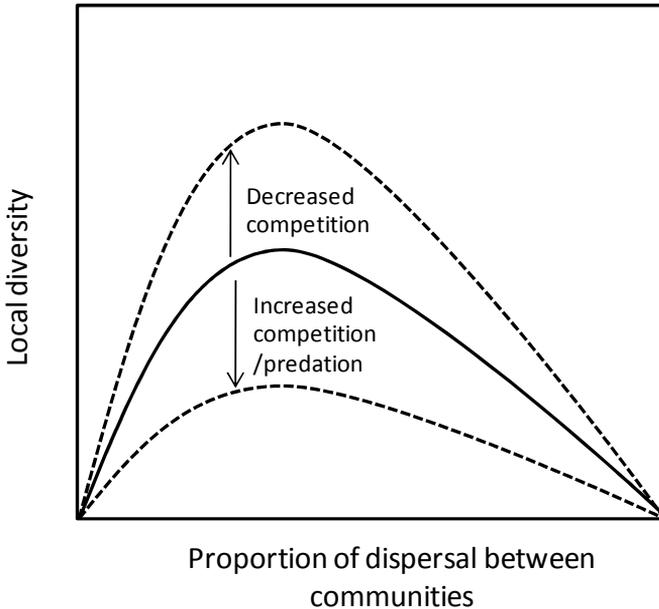


Figure 2. Local species richness as a function of the proportion of dispersal between communities. The solid line is here used as a baseline and show that local diversity is greatest at intermediate level of dispersal. If competition increases between species this will dampen the relationship and if competition (as a result of key-stone predation) decreases this elevate the relationship. Modified from Mouquet and Loreau (2002).

Negative effects of dispersal

Even though dispersal has been shown to be beneficial for population and community persistence in many cases, losses during dispersal is likely to occur making dispersal risky (Gaines & McClenaghan 1980). Even for species known for their migratory habits, the cost of dispersal may be considerable (Loxdale et al. 1993). Long-range movement occurs between different populations and takes place relatively infrequently compared to short-range movement within populations. The risk of dispersal should also increase with distance travelled. It has been shown that the probability of survival decreases with increased dispersal distance in studies of several different species groups such as marine invertebrates (Cowen et al. 2000), plants (Nathan 2006) and small mammals (Gaines & McClenaghan 1980).

Even small amounts of dispersal can sometimes cause decreased stability, diversity and productivity. When communities go from stable, well mixed to spatially structured, negative effects such as loss of diversity can occur (Saxer et al. 2009). Saxer et al. (2009) used microbial communities with different morphotypes of *E.coli* where the types (species) had benefits of being well mixed. The loss of diversity was due to interruption of positive species interactions when distance between populations increased with increased spatial division. Results like this point at the mechanisms behind some of the negative effects of habitat fragmentation. In a study of plankton communities where the initial communities were supersaturated (here: the number of species is greater than the number of limiting resources) introduction of dispersal, even at very low rates, resulted in loss of diversity (Roelke & Eldridge 2008). Important to note here is that in both studies mentioned the initial communities have been stable assemblages of interacting species, an important difference from most of the studies indicating benefits of introduction of spatial structure and dispersal.

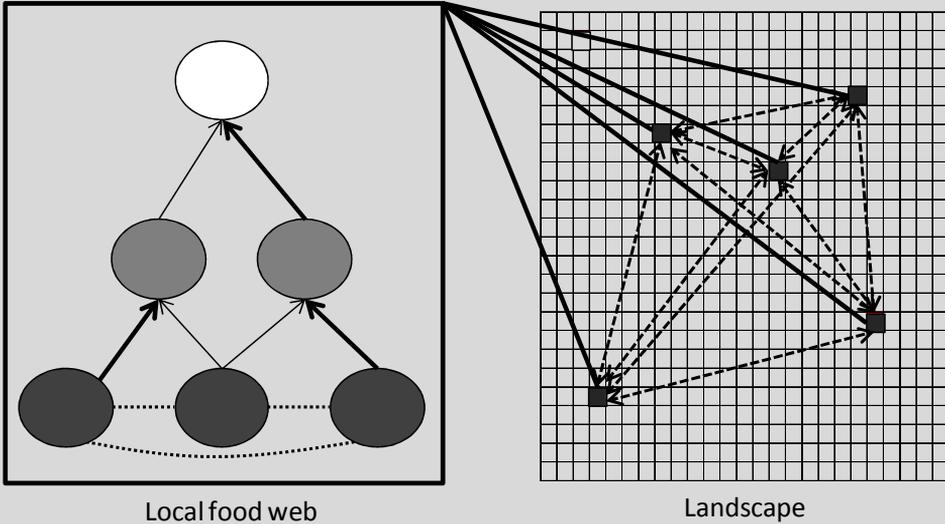
Summary of the metacommunity studies in thesis

A large part of the work with this thesis has been to develop a model combining local and regional processes in ecological communities. This model is used in *Papers IV* and *V*. Box 3 shows a schematic description of the model, for a more detailed description see *Paper V*. Here I summarize our findings and connect it to the reasoning in earlier sections.

We study food webs that are trophically more complex compared to those used in earlier studies (see former sections). The local food webs consist of six species interacting over three trophic levels. We model space explicitly and let the local communities be connected by dispersal of all species. As mentioned above, in most other studies the initial communities have been unstable (competitor or consumer-resource pairs not able to coexist in closed single patch communities) (Holyoak & Lawler 1996a; Loreau & Mouquet 1999; Amarasekare & Nisbet 2001; Amarasekare 2003) or populations have been 'forced' to oscillating dynamics in order to investigate synchrony patterns (Blasius et al. 1999; Koelle & Vandermeer 2005). In *Papers IV* and *V* we have taken a different approach and assumed initial communities to be stable and persistent in a closed setting.

Paper IV is strongly connected to *Paper I* in the sense that we investigate how food webs of different complexity (connectance) respond to the global loss of a species. However, in *Paper IV* we are interested in how the introduction of space and species dispersal affects this response. We find that the inclusion of space significantly reduces the risk of global and local cascading extinctions. It is shown that communities with low connectance are the most sensitive to species loss, but also that they are particularly well stabilized by the introduction of space. In agreement with theoretical studies of non-spatial

Box 3: Metacommunity model



Schematic description of the metacommunity model. Here is an example with a six species food web (three basal, two intermediate and one top species) and a landscape with five patches. Firstly, a local food web is constructed where all species can coexist as a closed community. Solid arrows represent feeding interactions and dotted lines represent interspecific competition between all basal species. Secondly, habitat patches are randomly placed in a grid (here 25 cells times 25 cells). The food web is replicated s times and one replica is placed in each habitat patch. Dispersal is allowed between all habitat patches, here represented by the broken lines in the landscape, and the species dynamics is observed.

habitats (Borrvall et al. 2000, *Paper I*), species at the highest trophic level are the most vulnerable to secondary extinction. This is particularly pronounced in spatial habitats, where the top predators appear to be the least well adapted to exploit the stabilizing properties of space.

In *Paper V* we investigate how a set of coexisting species are affected by introduction of space and species dispersal. Here we assume that dispersal involves a risk for the dispersers and show that this strongly affects the local

and regional persistence of the species. We investigate how the complexity of local communities, the spatial structure of the metacommunity and the dispersal characteristics of species affect species' extinction risks. In line with earlier studies (for example Amarasekare & Nisbet 2001; Loreau et al. 2003) we find that dispersal promotes local species diversity if dispersal rate is relatively low and movements are local while it has negative effects if dispersal rate is high and movements are global. The connectivity of the landscape has been shown to be important (Holyoak 2000a) and we find that high patch density promotes local species diversity. The regional processes have a stronger effect on complex local communities compared to simple ones. This implies that how species interact in a local food web is of importance for the response to dispersal. Also, here the top predators are most vulnerable to extinction. An important exception from *Paper IV* is, however, that in *Paper V* the system is not exposed to species removal. This indicates vulnerability for top predators in general.

Future directions

For future studies, there are some research topics that are especially interesting continuations of the work presented in this thesis.

Firstly, our model does not include any form of stochasticity. In natural communities stochasticity is probably an important factor because of, for example, seasonal and year to year variations in abiotic factors. Also, in the light of climate change the nature is supposed to be increasingly variable (IPCC 2007) and knowledge of how ecological communities respond to these changes is of major importance (Jentsch et al. 2007; Willis & Bhagwat 2009).

Secondly, in the landscapes we use, the habitat patches are randomly distributed and we replicate a lot of landscapes in order to capture a wide range of patch distributions. Nevertheless, it would be interesting to produce landscapes of different degrees of patch aggregation, from uniform to highly

aggregated, to evaluate the significance of how habitats are distributed (Lindström et al. 2008). It is suggested that some patches can play key-roles for the functioning of metacommunities (Bodin & Norberg 2007). Instead of (or in combination with) disturbing the metacommunities by species removal, disturbance by patch removal would give insights about the concept of key-patches. This is of major importance for conservation strategies in a time where habitat destruction is one of the largest threats to our planet (Sala et al. 2000).

Thirdly, in our model all species have equal dispersal abilities both concerning effective dispersal distance and rate of migration. Since it is well known that species at higher trophic levels move over larger areas (McCann et al. 2005; Rooney et al. 2008) a natural way to add more realism in our work would be to let dispersal distance be a function of trophic level.

Finally, in almost all investigations of ecological communities there has been a prime focus on predator prey links. However, ecological communities consist of a variety of other kinds of species interactions such as parasitism, pollination and mutualism. These links are important for community persistence (Fortuna & Bascompte 2006; Bascompte 2009; Bastolla et al. 2009; Lafferty & Kuris 2009). In order to develop more realistic models and increase our understanding of ecological communities incorporation of these interactions is important.

Acknowledgement

I am most thankful to my supervisor, Bo Ebenman, for your scientific guidance, encouragement and patience and for all the opportunities you have given me to work and develop in this exciting area of research. I am also very grateful to my second supervisor, Peter Münger, for all the hours we have spent in front of the computer, for your encouragement and never ending patience.

I also want to thank all people in the Theoretical Biology group for interesting discussions and a lot of fun! I will miss you all! And a special thank

you to my roommate, Linda Kaneryd, for always being encouraging and keeping up with my mixed mood during the last months. Thank you also all people at the Biology Department for friendship and nice discussions. And a special thank you to Annelie Andersson for being such a wonderful friend.

To my former colleague and roommate, Maria Christianou: Thank you for all the nice chats about science and personal stuff and for always being a good friend. Also thank you to Lotta Borrvall and all other former colleagues for all support. I am also grateful to all members in the scientific working groups InterACT and Sizemic. You have been a great source of inspiration, fruitful discussions and fun.

To my parents, Bo and Barbro, thank you for always being so supportive and believing in me!

Finally, my greatest thanks to Pierre, Fanny and Tuva, for always being there as a never ending source of joy and love!

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