

Linköping Studies in Science and Technology  
Dissertation No. 1431

Dynamics of ecological communities in variable environments  
–local and spatial processes

Linda Kaneryd



**Linköping University**  
**INSTITUTE OF TECHNOLOGY**

Department of Physics, Chemistry and Biology  
Theoretical Biology  
Linköping University  
SE-581 83 Linköping, Sweden

Linköping, Mars 2012

Linköping Studies in Science and Technology, Dissertation No. 1431

Kaneryd, L. Dynamics of ecological communities in variable environments – local and spatial processes

Copyright © Linda Kaneryd, unless otherwise noted

Also available from Linköping University Electronic Press  
<http://www.ep.liu.se/>

ISBN: 978 – 91 – 7519 – 946 – 7

ISSN: 0345 – 7524

Front cover: Designed by Johan Sjögren, photo by courtesy of Dan Tommila

Printed by LiU-Tryck, Linköping 2012

## ***Abstract***

The ecosystems of the world are currently facing a variety of anthropogenic perturbations, such as climate change, fragmentation and destruction of habitat, overexploitation of natural resources and invasions of alien species. How the ecosystems will be affected is not only dependent on the direct effects of the perturbations on individual species but also on the trophic structure and interaction patterns of the ecological community. Of particular current concern is the response of ecological communities to climate change. Increased global temperature is expected to cause an increased intensity and frequency of weather extremes. A more unpredictable and more variable environment will have important consequences not only for individual species but also for the dynamics of the entire community. If we are to fully understand the joint effects of a changing climate and habitat fragmentation, there is also a need to understand the spatial aspects of community dynamics. In the present work we use dynamic models to theoretically explore the importance of local (Paper I and II) and spatial processes (Paper III-V) for the response of multi-trophic communities to different kinds of perturbations.

In paper I we investigate how species richness and correlation in species responses to a highly variable environment affect the risk of extinction cascades. We find that the risk of extinction cascades increases with increasing species richness especially when the correlation among species is low. Initial stochastic extinctions of primary producer species unleash bottom-up extinction cascades, where specialist consumers are especially vulnerable. Although the risks of extinction cascades were higher in the species-rich systems, we found that the temporal stability of aggregate abundance of primary producers increased with increasing richness. Thus, species richness had a two-sided effect on community stability. Also during the extinction cascades it is possible that more robust species and interaction patterns will be selected which would further act to stabilize the post-extinction communities. In paper II we explore how the process of disassembly affects the structure of the interaction network and the robustness of the community to additional disturbances. We find that the disassembled communities are structurally different and more resistant to disturbances than equally sized communities that have not gone through a phase of disassembly. The disassembled communities are topologically as well as dynamically more stable than non-disassembled communities.

In paper III, IV and V we expand the analysis to incorporate the spatial dimension. In paper III we analyze how metacommunities (a set of local communities coupled by species dispersal) in spatially explicit landscapes respond to environmental variation. We examine how this response is affected by varying 1) species richness in the local communities, 2) the degree of correlation in species response to the environmental variation, between species within patches (species correlation) and among patches (spatial correlation) and 3) dispersal pattern of species. First we can confirm that our previous findings from paper I regarding local species richness and correlation among species within a patch are robust to the inclusion of a spatial dimension. However our results also show that the spatial dynamics are of great importance: first we find that the risk of global extinctions increases with increasing spatial correlation. Second we find

that the pattern and rate of dispersal are important; a high migration rate in combination with localized dispersal decrease the risk of global extinctions whereas a global dispersal pattern increases the risk of global extinctions. When dispersal is global the subpopulations of a species become more synchronized which reduces the potential for a patch to become recolonized following extinctions. We also demonstrate the importance of both local and spatial processes when examining the temporal stability of primary production at the scale of metapopulations, local communities and metacommunities.

In paper IV we investigate how the spatial structure of the landscape (number of patches) and dispersal pattern of species affect a metacommunities response to increased mortality during dispersal and local loss of species. We find a two-sided effect of dispersal on metacommunity persistence; on the one hand, high migration rate significantly reduces the risk of bottom-up extinction cascades following the removal of a species when dispersal involves no risk. On the other hand, high migration rate increases extinction risks when dispersal imposes a risk to the dispersing individuals, especially when dispersal is global. Species with long generation times at the highest trophic level are particularly vulnerable to extinction when dispersal involves a risk. These results suggest that decreasing the mortality risk of dispersing individuals by constructing habitat corridors or by improving the quality of the habitat matrix might greatly increase the robustness of metacommunities to local loss of species by enhancing recolonisations and rescue effects.

In paper V we use network theory to identify keystone patches in the landscape, patches that are of critical importance for the local and global persistence of species in the metacommunity. By deleting patches one at a time and investigating the risk of local and global extinctions we quantified the importance of a patch's position in the landscape for the persistence of species within the metacommunity. A selection of indices were used including some local indices that measure the connectedness of a patch in the intact network and some indices which measure the decrease in a global index after the deletion of the patch from the network. Global indices are those that give an impression of the connectivity of the entire patch network. We find that deletion of patches contributing strongly to the connectivity of the entire patch network had the most negative effect on species persistence.

## ***Populärvetenskaplig sammanfattning***

Förlust av biologisk mångfald är ett av de mest akuta miljöproblemen idag. På grund av mänsklig påverkan så uppskattas den hastighet som arter dör ut med idag att vara ca 100-1000 gånger högre än den naturliga takten. Två av de främsta orsakerna till den snabba utarmningen av biologisk mångfald är förstörelse och fragmentering av naturliga biotoper samt förändringar i klimatet på grund av global uppvärmning. En ökad global temperatur orsakat av koldioxidutsläpp förväntas leda till en högre frekvens och intensitet av extrema väderhändelser. En högre variation i miljön kan leda till en ökad risk för att arter dör ut. Förlust av arter är en allvarlig störning på de ekologiska systemen. Arter interagerar med varandra både direkt och indirekt i näringsvävarna och om en art dör ut kan det utlösa en kaskad av sekundära utdöenden, vilket i sin tur kan få allvarliga konsekvenser för stabiliteten och funktionen i ekosystemen. För att kunna minimera förlust av fler arter är det av yttersta vikt att förstå hur olika typer av ekologiska system påverkas av olika typer av störningar. En stor utmaning inom ekologin är att utveckla metoder för att kunna förutsäga vilka typer samhällen som är mest sårbara men även vilka typer av arter som i högre grad utlöser sekundära utdöenden om de själva dör ut?

Arter interagerar också via spridning mellan olika habitat i ett landskap, så det är viktigt att ta hänsyn till de processer som äger rum i landskapet. Genom att använda oss av matematiska modeller av ekologiska system kan vi genomföra sårbarhetsanalyser av ekologiska samhällen, där vi undersöker hur ekologiska samhällens trofiska struktur (antalet arter, interaktionsmönster), arters spridningsförmåga och hur habitatet ligger placerat i landskapet påverkar samhällenas svar på en ökad variation i miljön, lokala artutdöenden samt förlust av habitat

Vi fann att ekologiska samhällen med hög artrikedom är särskilt känsliga för en hög variation i omvärlden, risken för utdöende kaskader ökar ju fler arter det finns i systemet och särskilt om arterna svarar olika på omvärldsvariationen. Samtidigt, ökar stabiliteten i total biomassa med en ökande artrikedom. Så beroende på vilket mått man använder för att uppskatta hur stabilt ett samhälle är så kan man få helt olika svar. Samhällen som tidigare blivit utsatt för störning och förlorat arter visade sig vara mer stabila än tidigare ostörda samhällen. Om de mest sårbara arterna och strukturerna försvinner i de initiala utdöendena kan ett samhälle organiseras om till att bli mycket mer stabilt mot nya störningar. Spridning mellan habitat visade sig vara mycket viktigt för att upprätthålla artrikedomen i ett landskap, men bara om spridningen är lokaliserad, där mest spridning i huvudsak sker mellan närliggande habitat. Om arter istället sprider sig lika mycket till alla habitat oavsett avstånd i landskapet, försvinner denna positiva effekt genom att det uppstår synkroni mellan populationerna i de olika habitaterna, vilket ökar risken för utdöenden. Om det är en risk med att sprida sig genom landskapet kan detta motverka de positiva effekterna av spridning, genom att en stor proportion individer dör under migrationen. För att identifiera habitat som kan vara särskilt viktiga för arters och samhällens överlevnad genomförde vi ett experiment där vi plockade bort habitat ett i taget och sedan utvärderade om det fanns något samband mellan ett habitats position i landskapet och risken för att arter ska dö ut. Vi fann att många av de mått vi använde för att beskriva positionen i landskapet var till viss del korrelerade mot arters utdöende risker.

## ***List of papers***

- I. Kaneryd, L., Borrvall, C., Berg, S., Curtsdotter, A., Eklöf, A., Hauzy, C., Jonsson, T., Münger, P., Setzer, M., Säterberg, T., and Ebenman, B. (2012) Species-rich ecosystems are vulnerable to cascading extinctions in an increasingly variable world. *Ecology and Evolution, In press*
- II. Kaneryd, L., Münger, P. and Ebenman, B. (2012) Robustness of food webs whose structures have been shaped by extinctions in the past  
*Submitted manuscript*<sup>1</sup>
- III. Kaneryd, L., Münger, P., Eklöf, A. and Ebenman, B. (2012) Risk of global extinctions in metacommunities exposed to a highly variable environment: the role of local and spatial processes. *Manuscript*
- IV. Eklöf, A., Münger, P., Kaneryd, L. and Ebenman, B. (2012) Can dispersal rescue metacommunities from extinction cascades? *Submitted manuscript*<sup>2</sup>
- V. Westwood, L., Kaneryd, L., Münger, P. and Ebenman, B. (2012) Keystone patches: upholding diversity in multitrophic metacommunities. *Manuscript*

## ***Contributions to the papers***

Linda Kaneryd contributed equally with coauthors in shaping the ideas, choice of methodological tools and formulation of the questions in papers I-III and V. LK developed computer codes for papers I-III and V together with coauthors. LK performed the analysis of the results for paper II-III and part of the analysis in paper I and V. LK made a major contribution in the writing of papers I-III and contributed in the writing of paper IV-V.

<sup>1</sup> Submitted to *Proceedings of the royal society B*

<sup>2</sup> Submitted to *Philosophical transactions of the royal society B*.

## ***Table of contents***

### ***Part one***

<b><i>1. Introduction</i></b>	<b><i>2</i></b>
<b><i>1.1 Local processes</i></b>	<b><i>3</i></b>
<i>Environmental variation</i>	<i>3</i>
<i>Biodiversity and stability</i>	<i>4</i>
<i>The role of community structure</i>	<i>5</i>
<b><i>1.2 Spatial processes</i></b>	<b><i>7</i></b>
<i>Metacommunities</i>	<i>7</i>
<i>Spatial synchrony</i>	<i>8</i>
<i>Dispersal</i>	<i>9</i>
<i>Habitat loss</i>	<i>10</i>
<b><i>2. Aims</i></b>	<b><i>11</i></b>
<b><i>3. Methods overview</i></b>	<b><i>13</i></b>
<b><i>3.1 Community dynamics</i></b>	<b><i>13</i></b>
<b><i>3.2 Disturbances</i></b>	<b><i>15</i></b>
<b><i>3.3 Analyses</i></b>	<b><i>16</i></b>
<b><i>4. Results and Discussion</i></b>	<b><i>17</i></b>
<b><i>4.1 Local processes</i></b>	<b><i>17</i></b>
<b><i>4.2 Spatial processes</i></b>	<b><i>24</i></b>
<b><i>5. Concluding remarks</i></b>	<b><i>28</i></b>
<b><i>6. Acknowledgements</i></b>	<b><i>28</i></b>
<b><i>7. References</i></b>	<b><i>29</i></b>

### ***Part two***

***Paper I***  
***Paper II***  
***Paper III***  
***Paper IV***  
***Paper V***

## ***1. Introduction***

The growing human population is currently inducing a heavy load of perturbations on the ecosystems of our world. Some of the most severe threats are the destruction and fragmentation of natural habitats and the impact of climate change (Pereira et al. 2010). One of the major challenges for ecologists is to be able to forecast what the consequences will be for the stability and persistence of the species inhabiting our ecosystems. The biotic part of an ecosystem can be described by a food-web which depicts the trophic interactions, or who eats whom within the system. However, species does not only interact by eating and being eaten, there are also non-trophic interactions present, such as direct competition or mutualism. An ecological community is a description of both the trophic and the non-trophic interactions in an ecosystem (Goudard et al. 2008). How a specific ecological community will react to perturbations will depend both on the nature of the perturbation but also on how sensitive the species inhabiting the community are to the specific perturbation (Ives et al. 2004). Due to the interdependence among species in ecological networks, the loss or even a change in the abundance of one species can cause a dramatic change in the abundance of directly as well as indirectly interacting species. In the worst case an initial loss of one species can cause a cascade of secondary extinctions throughout the community (Pimm 1980, Borrvall et al. 2000, Dunne et al. 2002b, Ebenman et al. 2004, Ekloef et al. 2006, Petchey et al. 2008, Dunne et al. 2009, Fowler 2010, Stouffer et al. 2011). The severity of these extinction cascades will depend on the characteristics of the initially extinct species but also on the structure and interaction patterns of the entire community (Ebenman et al. 2005, Montoya et al. 2006, Ebenman 2011). It is also important to gain understanding of how extinctions of species will change the topology of a community but most importantly what consequences this will have for the functioning and stability of the ecosystems.

The processes mentioned above take place at the scale of a local isolated community, since species are also interacting at larger scales via dispersal between habitat patches in the landscape, it is important to consider the processes that take place at the scale of the entire landscape. When taking spatial processes into account dispersal is an important component; the ability to disperse can vary among different species and between landscapes (Holyoak et al. 2005, Rooney et al. 2008). Also many anthropogenic disturbances have consequences at a larger spatial scale. In this thesis I have used theoretical models of ecological communities to investigate how they respond to different kind of perturbations caused by anthropogenic activities. In the first part of the thesis I focus on the importance of the processes at the scale of the local community, especially on how biodiversity and interaction patterns affect the stability and persistence of communities when exposed to a highly variable environment. The second part of the thesis also accounts for the spatial dynamics, thus linking together local and spatial processes.

## ***1.1 Local processes***

### ***Environmental variation***

The environment that affects the population dynamics of species is naturally variable and unpredictable. Usually there is a wide spectrum of environmental variables that can change both temporally and spatially, such as climatic factors (Ruokolainen et al. 2009). Variation in the environment can affect species vital rates directly or indirectly mediated through species interactions (Ives et al. 2004). Time series of an environmental variable is described by its mean and variance and also by the temporal autocorrelation or its colour. In nature many time series have been found to display a positive autocorrelation structure resulting in a red or pink colour, but there are also examples of those that display white (no autocorrelation) or blue coloured (negative autocorrelation)(Ruokolainen et al. 2009). How the extinction risk of a population will be affected by changes in the autocorrelation structure are dependent on the type of population dynamics a species exhibit (Ruokolainen et al. 2009, Ripa et al. 1996, Lögberg et al. 2012 ). Current climate change is not only causing a gradual change in mean conditions of climate variables but is also changing their variability and it might also be expected to change the autocorrelation structure (Easterling et al. 2000). The frequency and intensity of weather extremes have increased and will continue to do so if global warming progress as forecasted (Meehl et al. 2004, Intergovernmental Panel on Climate Change 2007, Jentsch et al. 2007, Bender et al. 2010, Min et al. 2011, Duffy et al. 2012). Increased variance in the environment can be expected to result in increased variation in the fecundity and survival rates of species causing population stability and long-run growth rates of populations to decrease (Boyce et al. 2006, Morris et al. 2008). In combination with demographic stochasticity and Allee effects this might lead to increased extinction risks of populations and species in ecosystems (Griffen & Drake 2008, May 1973a, Ruokolainen et al. 2007, Ruokolainen et al. 2008, Adler et al. 2008, Borrvall et al. 2008, Burgmer et al. 2011, Gravel et al. 2011).

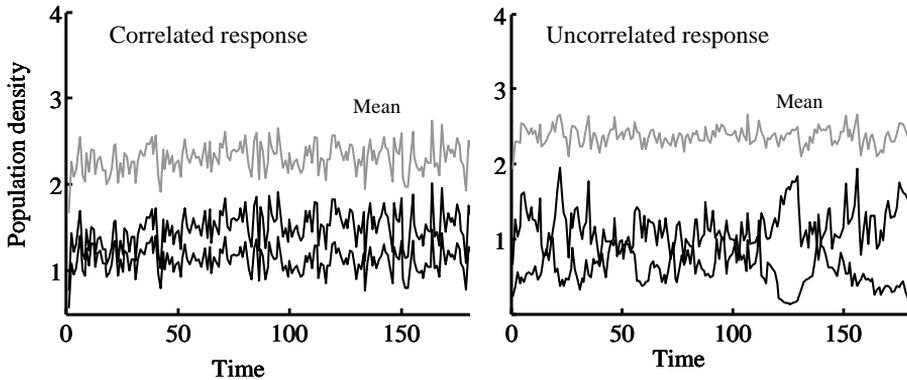
Species interact in complex networks and the loss of one species might in turn trigger a cascade of secondary extinctions (Pimm 1980, Borrvall et al. 2000, Dunne et al. 2002b, Ebenman et al. 2004, Ekloef et al. 2006, Petchey et al. 2008, Dunne et al. 2009, Fowler 2010, Stouffer et al. 2011). The risk and severity of extinction cascades are dependent on the structure of the community, such as its species richness and connectance, but also on the characteristics of the species initially lost (Ebenman et al. 2005, Montoya et al. 2006, Ebenman 2011, Curtsdotter et al. 2011). On the other hand environmental variation may, under certain conditions, facilitate the coexistence of competing species ((Gravel et al. 2011, Chesson et al. 1981, Adler et al. 2006). Here, one necessary condition is that each species must be able to increase in abundance when rare – the so called invasibility criterion (MacArthur et al. 1972). For this criterion to be fulfilled species must differ in their response to the environmental variability. Another factor important for the coexistence is the intensity and frequency of disturbances. Here coexistence has been shown to be maximized at an intermediate level of disturbance (Miller et al. 2011). Thus, theoretical work suggests that increased levels of environmental variability might either facilitate or impede the long-term coexistence of interacting species. Results from empirical studies are conflicting; for instance, temperature variability has been found to promote greater species richness (coexistence) in zooplankton communities in lakes

(Shurin *et al.* 2010) while reducing species richness and increasing extinction rates in microcosm phytoplankton communities (Burgmer *et al.* 2011). How ecosystems will respond to increased levels of environmental variability caused by global warming and how this response will be mediated by biodiversity and community structure is to a large extent an open question.

### ***Biodiversity and stability***

The impact of biodiversity on the stability and persistence of ecological communities has been a heavily debated question among ecologists for a long time (May 1973a, MacArthur 1955, Tilman 1996, McCann 2000, Ives *et al.* 2007). Historically, the view that diversity enhances stability was the predominating one before the 1970's when Robert May (1973) mathematically explored how diversity affects stability and found the opposite relationship that more diverse systems tends to be less stable (May 1973; McCann 2000). The discrepancy in this question stems from the numerous definitions of stability and that stability can be measured on different levels of ecological organization (Tilman 1996, Ives *et al.* 2007, Thebault *et al.* 2005). A stability measure that is commonly used in both theoretical and empirical studies is the temporal stability of abundance or biomass measured as the inverse of the coefficient of variation ( $1/CV$ ).

Species diversity is often positively related to stability measured as the aggregate density of the community as a whole; a requirement for this is that species respond differently to the environmental variation (Tilman 1996, Ives *et al.* 2007, Yachi *et al.* 1999, Ives *et al.* 2000, Elmqvist *et al.* 2003, Gonzalez *et al.* 2009, Jiang *et al.* 2009, Roscher *et al.* 2011). According to the insurance hypothesis (Yachi *et al.* 1999) if species respond differently to changes in the environment, the contribution of some species to ecosystem processes may decrease while the contribution of others may increase; this will reduce the temporal variability of an ecosystem property by creating negative covariances among populations (Figure 1). Increasing number of species should lead to a decreased variability in ecosystem processes because of increased probability for compensation among species (Yachi *et al.* 1999). But at the population level this insurance effect might increase the variability in abundance over time as diversity increases (Jiang *et al.* 2009, Lehman *et al.* 2000). Also the mean densities of each species tend to be lower in species-rich systems, due to density compensation caused by an increased intensity of competition (Gonzalez *et al.* 2009). These are factors that might cause increased extinction rates in more species rich systems.



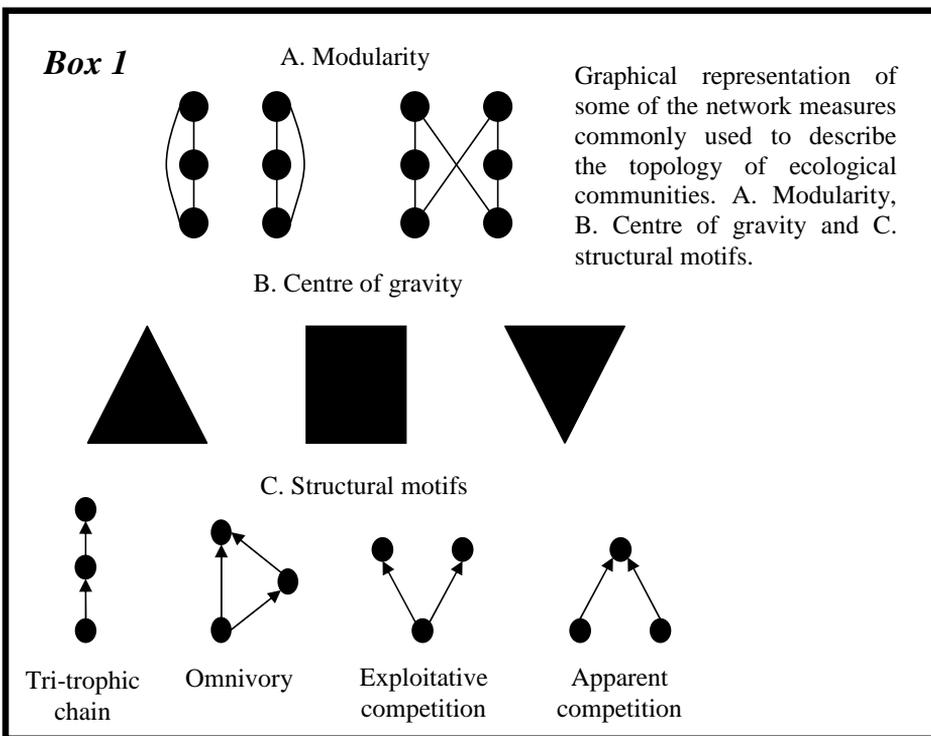
**Figure 1.** Time series of two species responding in a correlated (left panel) or uncorrelated (right panel) way to the environmental variation. The grey line represent the aggregated abundance (shifted upward for readability) of the two species.

Measuring the risk and extent of extinction cascades is another way of measuring how stable an ecological community is to different kinds of perturbations. By performing a “community viability analysis”, or CVA, one can evaluate how sensitive different types ecological communities are to the loss of certain species (Ebenman et al. 2004, Ebenman et al. 2005). Previous theoretical work have suggested that extinction cascades following species deletions should be less likely to occur in species-rich communities compared to species poor ones in an constant and deterministic environment, in the absence of any demographic or environmental stochasticity (Borrvall et al. 2000, Ebenman et al. 2004, Dunne & Williams 2009) . However including demographic stochasticity in one of these studies, revealed that species-rich systems had a much higher risk of quasi-collapse (the risk that the number of species falls below a given level) than in the absence of demographic stochasticity (Ebenman et al. 2004).

### ***The role of community structure***

Both the composition and the interaction patterns of species within ecological communities are important for their stability and persistence. When describing the topology of an ecological community the basic structures of a community, such as the number of species ( $S$ , as discussed above), links ( $L$ ) and connectance ( $C$ , number of links  $L$  divided by the number of possible links  $S^2$ ) are accounted for. These topological properties are relatively easy to derive from natural communities. By using a modelling approach one can test how these basic structures observed in natural communities relates to their stability and persistence. The connectance for example has been shown to increase the robustness of ecological communities to species deletions (Ekloef et al. 2006, Dunne et al. 2002a, Dunne & Williams 2009). Apart from measuring the connectance it is also important to understand how the links are distributed throughout the community. Many of the network measurements used in ecological research today have originated from graph theory and social sciences (Strogatz 2001). For instance the

distribution of number of prey and predators per species (degree distributions) (Dunne et al. 2002a, Camacho et al. 2002, Stouffer et al. 2005) the prevalence of structural motifs (Box 1) (Milo et al. 2002, Stouffer et al. 2007, Kondoh 2008, Stouffer et al. 2010), and degree of modularity (compartmentalization) (Box 1) (Stouffer et al. 2011, Pimm et al. 1980, Guimerà et al. 2010, Thebault et al. 2010). The above mentioned network properties are represented in natural communities and have been theoretically shown to affect their stability and persistence. Not only the number of species, but also the distribution of species at different trophic levels can have important implications. A measure that describes the shape or the distribution of species along a bottom to top axis in the community is the centre of gravity (CG) (Box 1) (Fussmann et al. 2002). Communities with a more triangular shape i.e. lower centre of gravity were found to be more resistant to species deletions (Borrvall et al. 2000, Ekloef & Ebenman 2006) and to be less prone to chaotic dynamics (Fussmann et al. 2002) than rectangular webs with a high centre of gravity.



To better understand the impacts of species loss from ecological communities it is important to gain insight in how community composition and the structure of the interaction network change during the process of disassembly and how these changes in turn affect the functioning and stability of the disassembled communities (Ives et al. 2004, Saavedra et al. 2008, Bascompte et al. 2009). Studies focusing on the disassembly of ecological networks have mainly been based on topological analysis performing

sequential deletions following a predefined order, such as the degree of specialization or connectivity of species within the network (Dunne et al. 2002b, Solé et al. 2001, Dunne & Williams 2009). These studies reveal that ecological networks tend to be robust to the loss of the most specialized or least connected species but sensitive to the reversed order where the most generalized and most connected species are targeted (Dunne et al. 2002b, Solé et al. 2001). Using a more ecologically realistic approach by ordering species by their environmental tolerances in 34 freshwater, pelagic food webs, Srinivasan et al. (2007) found that food webs were very robust to the extinction order spanning from least to most tolerant but highly sensitive to the reverse order. Similarly de Visser et al (2011) found the Serengeti food web to be very robust to a realistic deletion sequence based on species IUCN Red List Status, but very sensitive to a sequence spanning from most to least connected, which is in line with results from previous studies (Dunne et al. 2002b, Solé & Montoya 2001, Dunne & Williams 2009). Although robust to the realistic deletion sequence de Visser et al (2011) observed structural (topological) changes to the Serengeti food web, changes that might affect its robustness to future perturbations.

## ***1.2 Spatial processes***

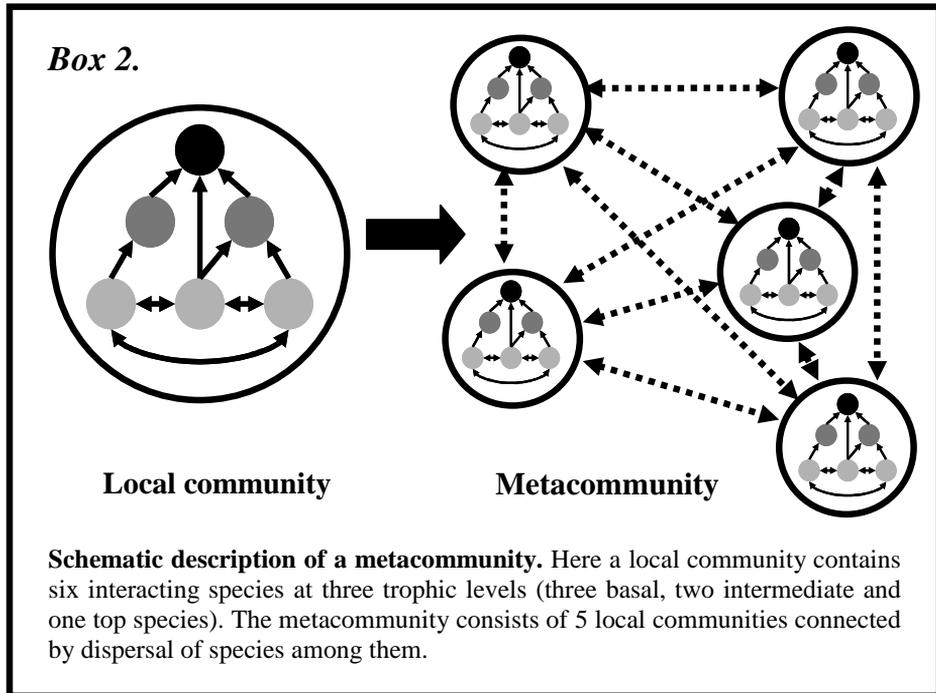
### ***Metacommunities***

Much theory in community ecology has focused on the dynamics at the local scale, assuming that local communities are closed and isolated. In nature ecological communities are more likely to exist as a network of several local communities that interact via dispersal of species. Such a network of local communities is called a metacommunity which is defined as a set of local communities that are linked by dispersal of multiple potentially interacting species (Box 2) (Wilson 1992, Holyoak et al. 2005, Leibold et al. 2004,). When studying metacommunities the dynamics affecting diversity and species persistence can be viewed at two different scales; the local scale and the regional scale. Local processes are governed by the trophic structure of the local communities (see section 1.1 above) and regional processes are governed by the spatial distribution of patches within the landscape and the dispersal abilities of species (Holyoak et al. 2005, Leibold et al. 2004).

In an influential review Leibold et al. (2004) proposed four perspectives for metacommunity research; patch-dynamic-, species-sorting-, mass-effect- and the neutral perspective. The purpose was to provide a broad conceptual framework for the theoretical and empirical work on metacommunities. The four perspectives differ in how metacommunity characteristics are defined. The main differences are the timescale of processes (species dynamics vs. dispersal), traits of species (competitive ability, dispersal rates), quality of patches (homogenous or heterogonous patches) and the prevalence of spatial synchrony. However as pointed out in this review it is more likely that a synthetic approach that link these perspectives together would provide a more realistic framework for understanding spatial dynamics and the response of metacommunities to perturbations (Leibold et al. 2004).

The response of a metacommunity to different kinds of perturbations will depend on the interactions among species within the local communities as well as on the spatial

distribution of patches within the landscape and the dispersal abilities of species. One of the major perturbations affecting the ecosystems is destruction and fragmentation of natural habitats causing population and species extinctions risks to increase (Holyoak et al. 2005). It is therefore important to investigate how metacommunities respond to species extinctions and habitat loss (Pimm et al. 2000).



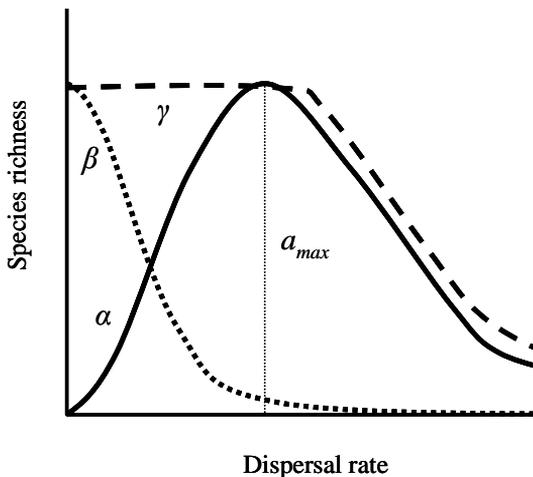
### ***Spatial synchrony***

Spatial synchrony occurs when densities of species populations in the different patches of the metacommunity fluctuate synchronously. Spatial synchrony can be caused by synchronous environmental factors (Moran 1953, Lande et al. 1999, Hudson et al. 1999, Abbott 2007), dispersal among local populations (Lande et al. 1999, Ranta et al. 1998, Bjørnstad et al. 1999, Liebhold et al. 2004, Goldwyn et al. 2008) or trophic interactions with other species (Small et al. 1993, Ims et al. 2000). Spatial synchrony caused by synchronous environmental factors (Lande et al. 1999, Hudson et al. 1999, Abbott 2007) is referred to as the “Moran” effect (Moran 1953) The “Moran” effect is in most systems considered to be the result of random but correlated climatic factors that influences communities or populations in a region. Dispersal among local populations can act to synchronize populations when an increase in density in one population produces emigrants that increase density in populations nearby (Holyoak et al. 1996). The synchronising effect of dispersal is most pronounced when the rate of migration is high (Lande et al. 1999, Ranta et al. 1998, Bjørnstad et al. 1999, Liebhold et al. 2004). Synchronous fluctuations can also exist among species that have direct trophic

interactions such as a predator and its prey. A wide-ranging predator could potentially act to synchronize the dynamics of its prey species in several locations (Small et al. 1993, Ims et al. 2000). A high degree of synchrony among the populations of a species in the different patches can lead to an elevated risk of global extinctions since all populations are small at the same time (Lande et al. 1999, Hudson et al. 1999, Abbott 2011). The general prediction from metapopulation theory state that increasing dispersal rate increases spatial synchrony and hence decreases the persistence of the metapopulations (Liebhold et al. 2004). When we move from metapopulations to a metacommunities the interactions among species within the local communities also needs to be considered (Melian & Bascompte 2002).

### **Dispersal**

Dispersal can also promote persistence, since dispersal makes it possible for a species to recolonize a patch following a local extinction. A requirement for dispersal to promote persistence is that the populations of a species are not perfectly synchronized across the landscape (Abbott 2011). Again the rate of dispersal is important; intermediate rates of dispersal can promote coexistence among species that are unable to coexist in closed communities and thereby enhance the diversity of species within local communities (Holyoak et al. 1996, Levin 1974, Caswell 1978, Amarasekare et al. 2001, Kerr et al. 2002, Mouquet & Loreau 2002, Kneitel & Miller 2003, Cadotte 2006, Amarasekare 2008, Hunt & Bonsall 2009) while low rates of dispersal might not be sufficient enough to allow recolonisations and high rates of dispersal might lead to synchronised local populations (Figure 2).



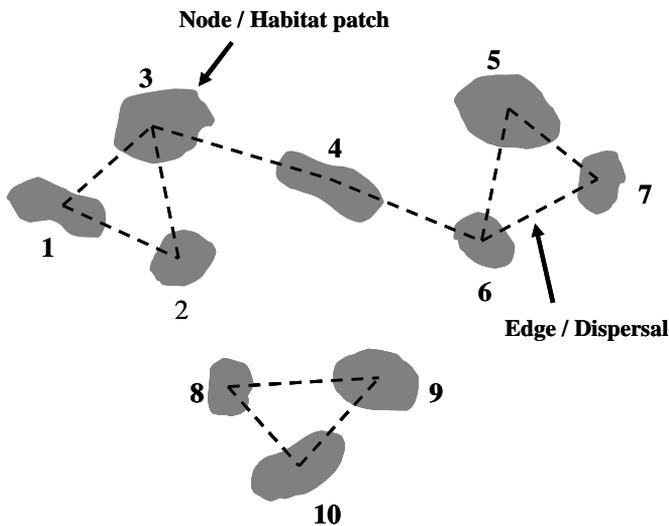
**Figure 2.** Species richness as a function of the rate of dispersal between local communities. Solid line = local diversity ( $\alpha$ ); dotted line = between community diversity ( $\beta$ ); dashed line = regional diversity ( $\gamma$ ).  $a_{max}$  is the dispersal value at which species diversity is maximal. Modified from Mouquet and Loreau, 2003.

Depending on the characteristics of the landscape, dispersal might pose a risk to the dispersing individuals (Gaines et al. 1980) and this risk is likely to increase with the distance traveled (Ruxton et al. 1997, Cowen et al. 2000, Nathan et al. 2008). When species disperse between patches of suitable habitat they might be forced to move across areas that are non-suitable or even hostile. Increased distance between habitats forces the

dispersing individuals to spend longer time in these hostile areas and hence decrease their chance of surviving the dispersal phase. If the mortality during dispersal is high then recolonisations and rescue mechanisms might no longer be effective.

### **Habitat loss**

Network theory can also be used to analyze the potential consequences of habitat loss. In landscape ecology and conservation biology network measures used to describe and assess the connectivity or probability of movement of species in a landscape originate from graph-theory (Urban & Keitt 2001, Bodin & Norberg 2007, Estrada & Bodin 2008). In landscape ecology a graph represents a landscape of discrete habitat patches as a set of nodes connected to some degree by edges between them (Fig. 3). An edge between two nodes implies that there is some kind of flux between those nodes, here dispersal of species between the two patches. A graph is connected if an edge exists between each pair of nodes, that is, if species can disperse among all patches in the landscape. In an unconnected graph species are unable to disperse among all patches in the landscape, which can contain several components (Fig. 3) (Minor et al. 2007).



**Figure 3.** A graph (landscape) consisting of 10 nodes (habitat patches) connected by edges (dispersal links) between them. The graph contains two components, nodes 1-7 and 8-10 (modified from Minor and Urban 2007)

The position of individual habitat patches in the landscape can be used to understand how the specific patch contributes to the overall connectivity of the landscape. In order to preserve the functionality of a landscape it is important to be able to assess how the connectivity is affected by the loss of a single patch (Bodin & Norberg 2007). The indices available to assess connectivity can be divided in two groups; local indices measuring the connectivity of each patch and global indices measuring the connectivity

of the whole patch network (Estrada & Bodin 2008).

To assess the importance of specific patches in upholding connectivity the approach differs between these two groups of indices. The use of global indices involves patch deletion experiments where the importance of each patch is quantified as the decrease in the global indices following deletion of the patch (Urban et al. 2001, Saura et al. 2007, Bodin et al. 2010). Local indices instead measure the importance of each and every patch within the intact landscape. Usually this involves assessing the centrality of a patch in the landscape, how much a specific patch is contributing to the dispersal flow throughout the landscape (Estrada & Bodin 2008, Freeman 1978).

Traditionally there has been a discrepancy between studies focusing on structural characteristic of the landscape and those explicitly modelling the dynamics of species and communities. In the framework of metacommunities these two approaches could be combined by investigating the importance of the positions of the patches in the landscape for the dynamics and ultimately the persistence of species within metacommunities.

## **2. Aims**

The overall aim of the thesis is to investigate how ecological communities respond to different kind of perturbation, mainly environmental variation and loss of species and habitat. In the first part of the thesis I will focus on the importance of the processes at the scale of the local community (paper I-II). In the second part of the thesis I also accounts for the spatial dynamics, thus linking together the local and spatial processes (paper III-V).

### ***Paper I: Species-rich ecosystems are vulnerable to cascading extinctions in an increasingly variable world.***

The aims of paper I are to investigate how species richness and the degree of correlation in species responses to a highly variable environment affect the risk of extinction cascades and the temporal stability in aggregated abundance of primary producers.

### ***Paper II: Robustness of food webs whose structures have been shaped by extinctions in the past.***

In paper II we explore how extinctions of species in food webs, caused by exposure to environmental variation, change the topology of the webs. We further examine if food webs shaped by extinctions are more or less robust to new disturbances than equally sized webs that have not experienced extinctions.

### ***Paper III: Risk of global extinctions in metacommunities exposed to a highly variable environment: the role of local and spatial processes.***

In paper III we expand the model used in paper I to also incorporate the spatial dimension. We analyze the effects of a highly variable environment on the risk of global extinctions and temporal stability in abundance of primary producers (measured at different levels of spatial organization) of metacommunities in spatially explicit landscapes. We vary species richness and degree of correlation in species response to the

environmental variation (species correlation) within the local communities to see if our findings from paper I are also valid in a spatial context. We also investigate the role of spatial correlation, that is, the correlation among patches for each species. Finally, we investigate the influence of species dispersal patterns.

***Paper IV: Can dispersal rescue metacommunities from extinction cascades?***

In metacommunities the ability of species to disperse through the non-habitat (matrix) is crucial for recolonisations to take place and hence for the long-term global persistence of species. If the quality of the matrix is deteriorating species might experience an increased mortality during dispersal. The aim of paper IV is to investigate how the spatial structure of the landscape (patch density) and dispersal patterns of species (migration rate and dispersal distance) affect a metacommunity's response to local loss of species and to increased mortality of individuals during dispersal.

***Paper V: Keystone patches: upholding diversity in multitrophic metacommunities***

In paper V we use network theory to identify keystone patches in the landscape, patches that are of critical importance for the local and global persistence of species in the metacommunity. By deleting patches one at a time and investigating the risk of local and global extinctions we aim to quantify the importance of a patch's position in the landscape for the persistence of species within the metacommunity.

### 3. Methods overview

Throughout this thesis I have used theoretical models to simulate the dynamics of species within local communities and the spatial dynamics that take place at the scale of the landscape. Here I will give an overview over the methods used.

#### 3.1 Community dynamics

##### *Local community assembly*

Local communities are triangular in shape (i.e., decreasing number of species with increasing trophic level) with three trophic levels: primary producers, herbivores (primary consumers) and carnivores (secondary consumers). When varying the number of species ( $S$ ) in the webs the proportions of species at the different trophic levels are preserved in webs of different sizes (Paper I, II and III). Connectance ( $C$ ) – here defined as the number of trophic (consumer-resource) links ( $L$ ) divided by the number of species raised to two (i.e.  $C=L/S^2$ ), is kept constant for communities of different sizes (Paper I, II and III). A constant connectance means that the average number of links per species (link density) increases with increasing species richness. Trophic links are randomly allocated between species at different trophic levels. Carnivore species are potentially omnivorous. In paper I we model two cases of consumer preferences, 1) specialists (strong preference for one resource species) or 2) generalists (equal preference for each of their resource species). In paper II, III and IV all consumer species are specialist whereas in paper V we model a continuum of consumer types by randomly varying the preferences. There are also non-trophic interactions present: each primary producer species directly compete with all other primary producer species and direct intra-specific competition is present in all species.

##### *Modeling local community dynamics*

In this thesis I use theoretical models of multitrophic ecological communities, where the dynamics of species over time is described by the generalized Rosenzweig-MacArthur model (Rosenzweig & MacArthur 1963):

$$\frac{dN_i}{dt} = N_i \left( b_i(t) + \sum_{j=1}^S \tilde{a}_{ij} \cdot N_j \right) \quad (1)$$

here  $dN_i/dt$  is the rate of change of density of species  $i$  with respect to time in a community with  $S$  species,  $b_i(t)$  is the intrinsic per capita growth rate of species  $i$  at time  $t$ , and  $\tilde{a}_{ij}$  is the per capita effect of species  $j$  on the per capita growth rate of species  $i$ . The functional response of consumers is of type II, meaning that the per capita strength of trophic links,  $\tilde{a}_{ij}$ , is a function of the densities of resource species. The use of a functional response of type II is often more realistic than a response of type I (linear) where individual predators always consume the same fraction of the prey population irrespective of prey density. In a 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.

To attain some generality we assemble a large amount of replicate communities where the links and interactions strengths among species are sampled from predefined intervals. Before we expose the communities to disturbances we check that the communities can persist in a deterministic environment and in the absence of the disturbances. This is done by numerically simulate the replicate communities for a long period of time and then check that all species are alive at the end of the simulation. A species is considered extinct if its density falls below a specified quasi-extinction threshold. Defining quasi-extinction thresholds is a way of accounting for processes such as demographic stochasticity, inbreeding depression and potential Allee effects.

### *Spatial dynamics*

In papers III-V the model is expanded from a single isolated community to a system of local communities (a metacommunity) in a spatially explicit landscape. The landscape is a cell grid in which  $s$  patches (local communities) are allocated their positions in the grid randomly from a continuous uniform distribution. A system of  $s$  persistent local starting communities is assembled as above. Each local community has the same structure but can vary in the growth rate of the primary producers. Each patch is continually subject to migration events: per time unit, a fixed proportion,  $m$ , of each species' population migrates from its current patch and disperses among the other communities. For a landscape of  $s$  habitat patches, the number of individuals migrating from patch  $q$  to patch  $p$ , per unit time, is given by:

$$M_{i,p,q} = mN_{i,q} \frac{e^{-d_{p,q}/c_i}}{\sum_{l,l \neq q}^s e^{-d_{l,q}/c_i}} \quad (2)$$

where  $N_{i,q}$  is the density of species  $i$  in patch  $q$ , the distance between the two patches is  $d_{p,q}$  and  $c$  is a parameter (see (Hanski et al. 1993)). The parameter  $c$  allows us to vary the degree of distance dependence of dispersal. In paper III-IV we model two cases, local dispersal (low  $c$ ) and global dispersal (high  $c$ ). In paper V we use a different approach by assigning maximum dispersal distances to species ( $d_{max}$ ). The dispersal parameter  $c$  is then given by  $c = -d_{max} / \ln(0.2)$ . In paper III and V we assume that species at higher trophic level are able to disperse longer distances than species at lower trophic levels. This is implemented by increasing values of  $c$  (paper III) or  $d_{max}$  (paper V) with increasing trophic level. To avoid edge effects the dispersal kernel is used with periodic boundary conditions (Lindström et al. 2008). The change in species densities, per unit time, in patch  $p$  as a result of migration is then given by:

$$\tilde{N}_{i,p} = \sum_{\substack{q \\ q \neq p}}^s M_{i,p,q} - (mN_{i,p}) \quad (3)$$

where the summation term represent flux in and the second term flux out. The  $q \neq p$  condition on the summation term means that no migrant may return to the patch it has just vacated. The dynamics of species  $i$  in patch  $p$  is then given by:

$$\frac{dN_{i,p}}{dt} = N_{i,p} \left( b_i(t) + \sum_{j=1}^S \tilde{a}_{i,j} N_{j,p} \right) + \tilde{N}_{i,p} \quad (4)$$

### 3.2 Disturbances

#### *Environmental variation*

We introduce environmental stochasticity as white noise (i.e., no serial correlation) in the intrinsic growth rates (mortality rates);  $b_i(t) = \bar{b}_i(1 + \varepsilon_i(t))$  where  $\bar{b}_i$  is the mean value of the intrinsic growth rate of species  $i$  and  $\varepsilon_i(t)$  is a stochastic variable drawn from a distribution with minimum, mean and maximum values equal to -1, 0 and 1, respectively. In papers I-III and V we model a highly variable environment (variance of  $\varepsilon$  is equal to 0.333) where extreme values are as likely as the mean value. We use such a distribution because the aim of these papers is to explore how communities respond to highly variable environments in which extreme values are likely to occur. In paper II we also use a moderate level of variance in the environment (variance of  $\varepsilon$  is equal to 0.167). There are two types of correlation in the response of species to environmental variation, species correlation and spatial correlation. Species correlation quantifies the degree of correlation among species within a local community in their responses to environmental variation (Papers I-III and V). The spatial correlation quantifies the degree of correlation among the local populations of each species in the different patches (Paper III). In paper V the spatial correlation is assumed to be distance dependent such that populations in patches that lie close to each other experience the same environment and hence are more correlated than populations in patches that lie far away from each other.

#### *Species removals*

In paper II (single closed communities) and IV (metacommunities) we remove species from the model communities (forced extinctions), one species at a time. In paper IV species removal is partial; species are deleted from 50% of the local communities (patches) in the metacommunity. Thus, in paper II the forced extinctions are global, whereas in paper IV the extinctions are local and species are able to recolonize.

#### *Dispersal risk*

Dispersal might pose a risk to the dispersing individuals (Gaines et al. 1980) and this risk is likely to increase with dispersal distance (Ruxton et al. 1997, Cowen et al. 2000, Nathan et al. 2008). In paper IV we investigate how increased mortality during dispersal affects the local persistence of species in metacommunities and the ability of species to recolonize patches from which they have gone locally extinct. In paper V, where we

examine the importance of different patches for upholding the species diversity in the metacommunity, a dispersal risk is also included in the model.

### ***Patch deletions***

The position of a habitat patch in a landscape can be important for its role in upholding the local and global species diversity in the metacommunity. In order to quantify the importance of different patches for metacommunity persistence, that is, to identify keystone patches, we performed a patch removal experiment (Paper V).

## **3.3 Analyses**

### ***Extinctions and recolonizations***

Following the application of the different disturbance scenarios investigated in this thesis, the communities or metacommunities are simulated numerically over a relatively long period of time. During the simulations all extinction events are recorded and the probability of extinction for species at different trophic levels calculated. A species is considered extinct if its density falls below the specified quasi-extinction threshold. In metacommunities extinctions can be local meaning that the species go extinct in some of the habitat patches (paper IV-V) or global where species go extinct in all patches (paper III and V). When extinctions are local, species can recolonize patches from which they earlier went extinct. We therefore also measure the ability of species to recolonize (paper III and IV). In paper I-II communities are closed so here species extinctions are consequently of a global nature. In order to discover potential extinction cascades, we register the time of each extinction event during the simulations (paper I and III).

### ***Temporal stability in aggregate abundance***

A stability measure that is commonly used in both theoretical and empirical studies is the temporal stability of aggregate abundance of species or populations measured as the inverse of the coefficient of variation ( $1/CV$ , where  $CV$  is defined as the ratio of the standard deviation to the mean). In paper I we have measured the temporal stability of the aggregate abundance of the primary producers within a single closed community. In paper III we measure the temporal stability in aggregate abundance of primary producers at three levels: 1) metapopulation stability – the stability in the aggregate abundance of all local populations for each primary producer species; 2) local community stability – the stability in aggregate abundance of all primary producer species within each local community; and 3) metacommunity stability – the stability in the total aggregate abundance of all primary producer species across all patches.

### ***Synchrony between species and patches***

In paper I we measure the synchrony between the per capita growth rates of primary producer species over time using the pair-wise correlation (Pearson's correlation coefficient). For each replicate a pair of populations was chosen at random among the primary producer species in the web. The only criterion was that the primary producer species had to have survived for at least 100 time steps. This was to ensure that the time series would be long enough to give a reliable correlation value for the time series. In paper III we also measure the degree of synchrony in the per capita growth rates between

patches for each species (average metapopulation synchrony – synchrony across the 10 patches for each species (Loreau & De Mazancourt 2008).

### ***Web topology and topological robustness***

In paper II we quantify and compare the topology of food webs that have been shaped by extinctions (disassembled webs) and food webs that have not experienced extinctions (non-disassembled webs) by using different network measures. Following the exposure to disturbance we quantify the topological robustness in the two types of food webs by measuring the overall topological change in the webs. Topological robustness is calculated as the Euclidean distance between the pre- and post-disturbance webs in the multi-dimensional space defined by the network measures.

### ***Identifying keystone patches***

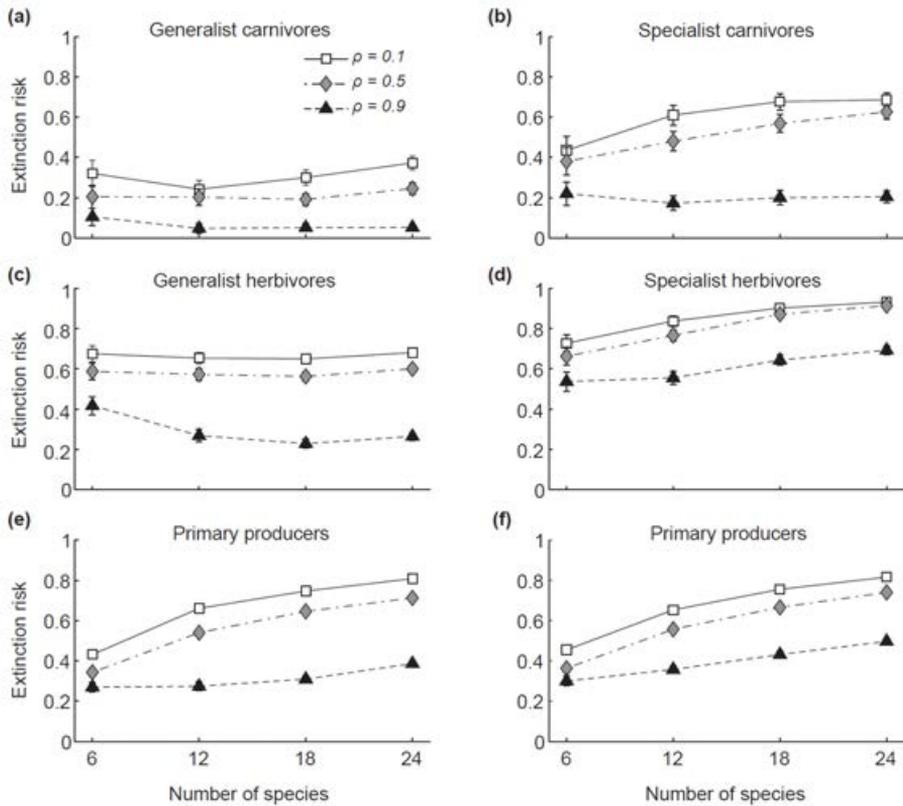
In paper V we investigate how a patch's position in the landscape affects its importance for upholding species diversity in the metacommunity. Those patches whose deletion causes the largest increases in local- or global extinction probability are those that have proven to be most important for upholding the diversity of the metacommunity. If we can find a network index that ranks these keystone patches higher than others then we would have a method of identifying them in real ecological networks. There has been much recent research on the application of network theory to ecological networks and many network indices exist to measure the properties of a network and its elements. We have used two types of indices; local indices measuring the connectivity of a patch and global indices measuring the connectivity of the whole patch network (Estrada & Bodin 2008).

## ***4. Results and Discussion***

### ***4.1 Local processes***

#### ***Biodiversity and the risk of extinction cascades***

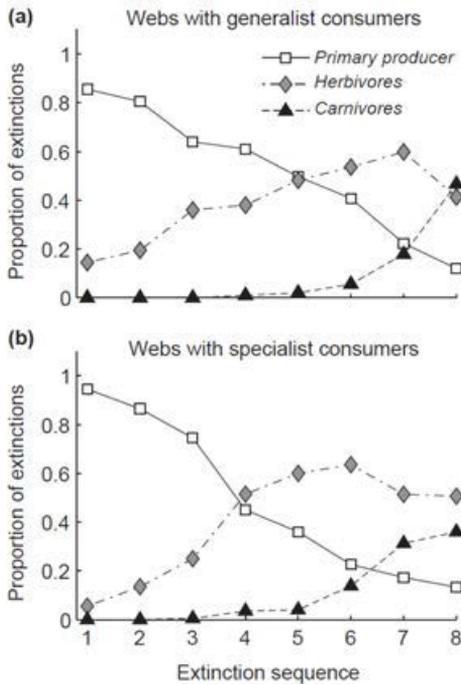
Earlier theoretical work have suggested that extinction cascades and community collapses following species deletions should be less likely to occur in species-rich communities compared to species poor ones in a constant and deterministic environment, that is, in the absence of demographic or environmental variation (Borrvall et al. 2000, Ebenman et al. 2004, Dunne & Williams 2009). In a highly variable environment we found that the risks of cascading extinctions were higher in species-rich communities than in species-poor ones (Figure 4, paper I).



**Figure 4.** Mean per species risk of extinction (bars show 95 % CI) for carnivores (a, b), herbivores (c,d) and primary producers (e,f) as a function of number of species in the food web. Left column (a,c,e) shows results for food webs with generalist consumers and right column (b,d,f) shows results for webs with specialist consumers. Series display the degree of correlation in species responses to environmental variation,  $\rho$ ;  $\rho = 0.1$  (solid line),  $\rho = 0.5$  (dash-dotted line) and  $\rho = 0.9$  (dashed line). Scenario: high environmental variation ( $\text{var}(\epsilon) = 0.33$ ) and weak intra-specific competition in consumers ( $a_{ii} = -0.001$ ). Results based on 200 independent replicate model food webs. Bars show 95 % CI.

An analysis of the temporal pattern of extinctions revealed that initial extinctions of primary producer species unleashed bottom-up extinction cascades (Figure 5, paper I). The secondary nature of herbivore and carnivore extinctions were also demonstrated by the fact that specialist consumers had a higher risk of going extinct compared to generalist consumers (Figure 4, paper I). Specialist consumers have a strong preference for one of their resource species, and are very dependent on that specific resource for survival. As a consequence, the loss of the preferred resource species almost inevitably leads to an extinction of a specialist consumer. Generalist consumers, on the other hand, are not dependent on one particular resource species and are less likely to go secondarily extinct following the loss of one of its resource species. This is in line with the argument put forward by MacArthur already in 1955: consumer species feeding on many resource species should be less affected by variation in resource abundances than consumers

feeding on few resource species. As the extinction risks of primary producer species increased with increasing species richness, so did the extinction risk of specialist consumers. Extinction risk of generalist consumers, on the other hand, was not strongly related to species richness (paper I, figure 4). Our findings are supported by a recent field experiment where the population stability of specialist herbivores were found to decrease with increasing plant species diversity while the population stability of generalist herbivores was unaffected or increased with increasing plant diversity (Haddad et al. 2011, Petchey 2000).



**Figure 5.** Proportion of extinctions affecting species at different trophic levels in the ordered sequence of extinctions in food webs with (a) generalist consumers and (b) specialist consumers. Extinctions early in the sequence are predominantly of primary producers while extinctions late in the sequence are mainly of consumer species (herbivores and carnivores). Original number of species in the webs is equal to 12. Scenario: low correlation in species responses to environmental variation ( $\rho = 0.1$ ), high environmental variation ( $\text{var}(\epsilon) = 0.33$ ) and weak intra-specific competition in consumers ( $a_{ii} = -0.001$ ). Results based on 200 independent replicate model food webs.

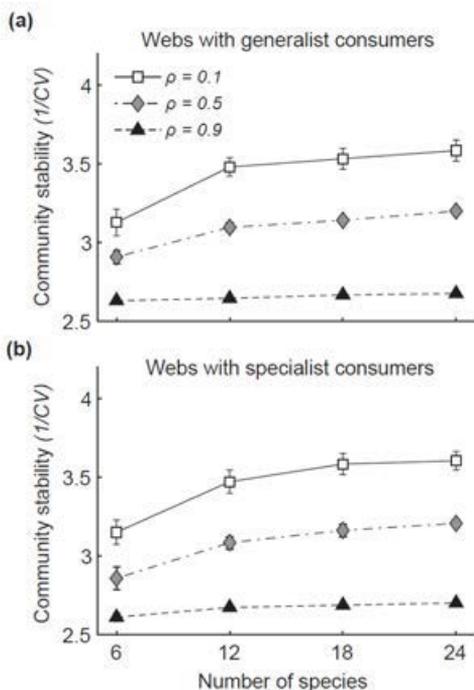
What mechanisms are involved in causing the initial extinctions of primary producers, unleashing the extinction cascades, and why are primary producers in species-rich communities more extinction prone than those in species-poor communities? We observed an inverse relationship between increasing species richness and the population densities of primary producers. This density compensation was caused by increased intensity of inter-specific competition among primary producers in species-rich communities (Ebenman et al. 2004, Borrvall et al. 2008). As a consequence the densities of primary producers are closer to the extinction threshold in species-rich than in species-poor communities resulting in an increased risk of extinction (paper I). Here we assumed that each primary producer species competed with all other primary producer species. If instead assuming a “niche based” type of competition, where each species only directly compete with a few neighbouring species, the relationship between species richness and

population densities might be much weaker (Hughes et al. 2000). The density of a primary producer could also be affected by predation pressure from its consumers. For any given level of species richness, a weak intra-specific competition in consumer species increased the per-capita predation pressure on primary producers, causing primary producers to be even closer to the extinction threshold (paper I).

Decreasing degree of correlation among species in their response to environmental fluctuations was also shown to increase the risk of extinction for primary producers which in turn increased the risk of extinction for consumer species (bottom-up extinction cascades). Low correlation among primary producer species in their response to environmental fluctuations leads to a low synchrony in their per capita growth rates (see. paper I). Under these conditions inter-specific competition among the primary producer species will amplify the environmentally driven population fluctuations (Tilman 1996, Thebault et al. 2005, May 1973b). In the presence of high environmental variation the amplitude of these fluctuations may become so large that the populations fall below the extinction threshold. Recent theoretical work on competition communities (one trophic level) exploring the effects of correlation among species, suggests that our findings are also valid for environments with red noise (temporal autocorrelation) (Ruokolainen et al. 2009, Ruokolainen et al. 2007, Ruokolainen et al. 2008, see Rukolainen *et al.* 2009 for a review). In our study the degree of correlation among species in their responses to the environmental fluctuations was not dependent on species richness. According to Elmqvist *et al.* (2003) response diversity is likely to increase with increasing species richness and hence correlation among species could be expected to decrease with increasing species richness. This might lead to even higher extinction risks in species-rich communities, since low a correlation per se leads to high extinction risks.

### ***Is there an insurance effect of biodiversity?***

The temporal stability of the aggregate density of all species within a community has been shown to be positively related to species-richness given that species respond differently to environmental variation (Tilman 1996, Ives et al. 2007, Yachi et al. 1999, Ives et al. 2000, Elmqvist et al. 2003, Gonzalez et al. 2009, Jiang et al. 2009, Roscher et al. 2011). Such response diversity will reduce the temporal variability at the community level by creating negative covariances among populations. Increasing species richness increases the probability for compensation among species which increases the stability at the community level (Yachi and Loreau 1999; Gonzalez and Loreau 2009). In the present work we found that the temporal stability of the aggregate abundance of primary producers increases with increasing species richness, especially when the correlation among species in their responses to environmental variation is low (figure 6). Thus, in this respect our results corroborate earlier theoretical studies suggesting that the insurance hypothesis should also be effective in multi-trophic communities (Thebault et al. 2005, Ives et al. 2000).

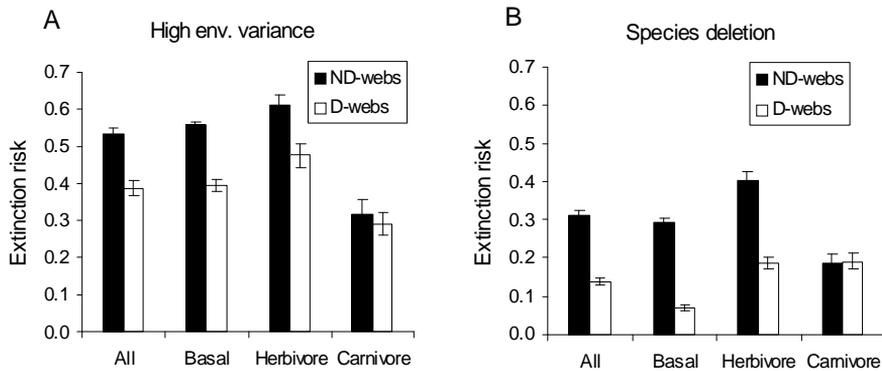


**Figure 6.** Temporal stability ( $1/CV$ ) (bars show 95 % CI) of aggregate abundance of primary producers in food webs with (a) generalist consumers and (b) specialist consumers. Series display the degree of correlation in species responses to environmental variation,  $\rho$ ;  $\rho = 0.1$  (solid line),  $\rho = 0.5$  (dash-dotted line) and  $\rho = 0.9$  (dashed line). Scenario: high environmental variation ( $\text{var}(\epsilon) = 0.33$ ) and weak intra-specific competition in consumers ( $a_{ii} = -0.001$ ). Results based on time series from 100 independent replicate model food webs.

The effects of biodiversity on the response of ecosystems to an increasingly variable environment is two-sided: exactly the same conditions – high species richness and low correlation in the responses of species to environmental variation – that lead to increased temporal stability of aggregate producer abundance results in increased risks of extinction cascades. Even though extinction risk per species is higher in species-rich communities than in species-poor ones they still have more species remaining in the post-extinction communities than do the species-poor communities. As a result they will still have a higher compensatory capacity than the species-poor communities.

### ***Robustness of communities shaped by extinctions in the past***

The fact that more species remains in species-rich than in species-poor communities following a long period of disassembly in a stochastic environment (paper I), implies that food webs might become more robust during the disassembly process. To examine this we compared the structure and robustness of food webs that were shaped by extinctions in the past (disassembled webs), to equally sized food webs that had not experienced extinctions (non-disassembled webs). We found significant differences in all of the network measures that were used to compare the structure of disassembled and non-disassembled food webs (paper II). To test the robustness of the two types of food webs we exposed them to two novel disturbances, species deletions and high levels of environmental variability. Overall, robustness to disturbances is higher in disassembled than in non-disassembled food webs (figure 7).

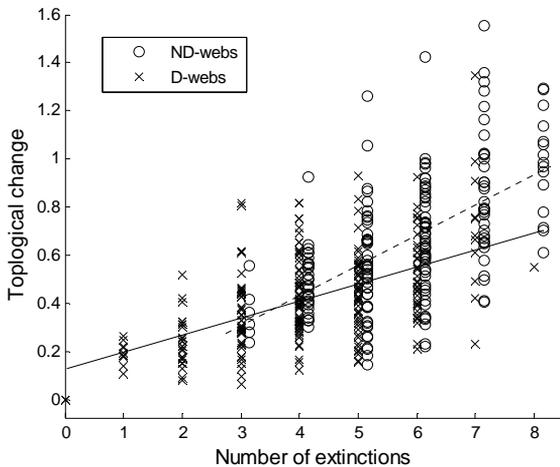


**Figure 7** Per species risk of extinction averaged over all species, primary producers, herbivore species and carnivore species, for non-disassembled communities (black bars) and disassembled (white bars). Disturbance scenarios: **A**, high environmental variability ( $\text{var}(\varepsilon) = 0.333$ ) and **B**, species deletions in a moderately variable environment ( $\text{var}(\varepsilon) = 0.167$ ). Correlation in species responses to environmental fluctuations,  $\rho$ , is equal to 0.3 and strength of intra-specific competition among consumers,  $a_{ii}$  is equal to -0.1. Error bars shows 95% confidence intervals.

Are the structural and compositional changes observed in the disassembled communities related to their robustness to further disturbances? On average, more primary producers than consumer species are lost during disassembly. Thus, a more rectangular web shape seems to increase the robustness of the disassembled communities to additional disturbances. This finding contrast to earlier theoretical work suggesting that communities with a more triangular shape, i.e., lower centre of gravity, should be more resistant to species deletions (Borrvall *et al.* 2000; Eklöf & Ebenman 2006) and less prone to chaotic dynamics (Fussmann & Heber 2002). However, in these studies communities were simulated in constant environments (deterministic setting), in the present work communities were exposed to a variable environment. Since all primary producer species compete with each other, the loss of species during disassembly means that the surviving primary producer species will experience a competitive release allowing their densities to increase (paper I). An increase in population densities following loss of competitors will make the surviving species less vulnerable to extinction (Ebenman *et al.* 2004, Gross *et al.* 2005). A decreased risk of stochastic extinction for primary producer species will in turn decrease the risk of bottom-up extinction cascades (paper I). Following extinctions of primary producers during the disassembly phase both the mean and the variance of the strength of competition among the remaining primary producer species becomes lower (paper II). A lower mean and variance of the strength of inter-specific competition has previously been shown to facilitate coexistence of species and stabilize competitive communities (Fowler 2010, Kokkoris *et al.* 1999, Kokkoris *et al.* 2002).

We also found that extinctions led to changes in the distribution of the trophic links at the different trophic levels in the food webs. Generality of carnivores was higher relative to that of herbivores and the vulnerability of primary producers was lower relative to that of

the herbivores in the disassembled webs compared to the non-disassembled webs (paper II). Gross and colleagues (2009) identified two general patterns regarding connectivity of species and stability in food webs: stability is enhanced if 1) generality of carnivores is high relative to that of herbivores and 2) vulnerability of herbivores is high relative to that of primary producers (Gross et al. 2009, Otto et al. 2007). We also found that the fraction of omnivorous links had increased following disassembly. Omnivory has earlier been reported to stabilize food webs (Borrvall et al. 2000, McCann et al. 1997). Moreover, the degree correlation becomes more negative following disassembly; this means that asymmetric links – links between species with high and low degree (number of links) – are preserved during disassembly. Such a pattern has been observed also in other kinds of networks following disassemble (Saavedra et al. 2008). A negative degree correlation indicates that the network is compartmentalized into modules (Melián et al. 2002), a pattern which has been found to stabilize ecological networks (Stouffer et al. 2011, Thebault & Fontaine 2010).



**Figure 8.** Relationship between number of extinctions and topological change for non-disassembled (circles, dotted regression line,  $R^2=0.341$ ) and disassembled communities (crosses, solid regression line,  $R^2=0.295$ ). Disturbance scenario: high environmental variability ( $\text{var}(\epsilon) = 0.333$ ). Correlation in species responses to environmental fluctuations,  $\rho$ , is equal to 0.3 and strength of intra-specific competition among consumers,  $a_{ii}$ , is equal to -0.1.

Several of the structural changes brought about by extinctions during disassembly are in a direction that has been reported to stabilize food webs. Not only are the disassembled food webs more dynamically robust to additional disturbances, they are also more topologically robust (paper II). Thus, there is a steeper increase in topological change with increasing number of extinctions in non-disassembled webs than in disassembled webs (Figure 8). To conclude, disassembled food webs are dynamically as well as topologically more robust to perturbations than non-disassembled webs (webs whose structure has not been shaped by extinctions in the past). This suggests that fragile interaction patterns are lost during the process of disassembly and consequently that structures promoting robustness are preserved.

## 4.2 Spatial processes

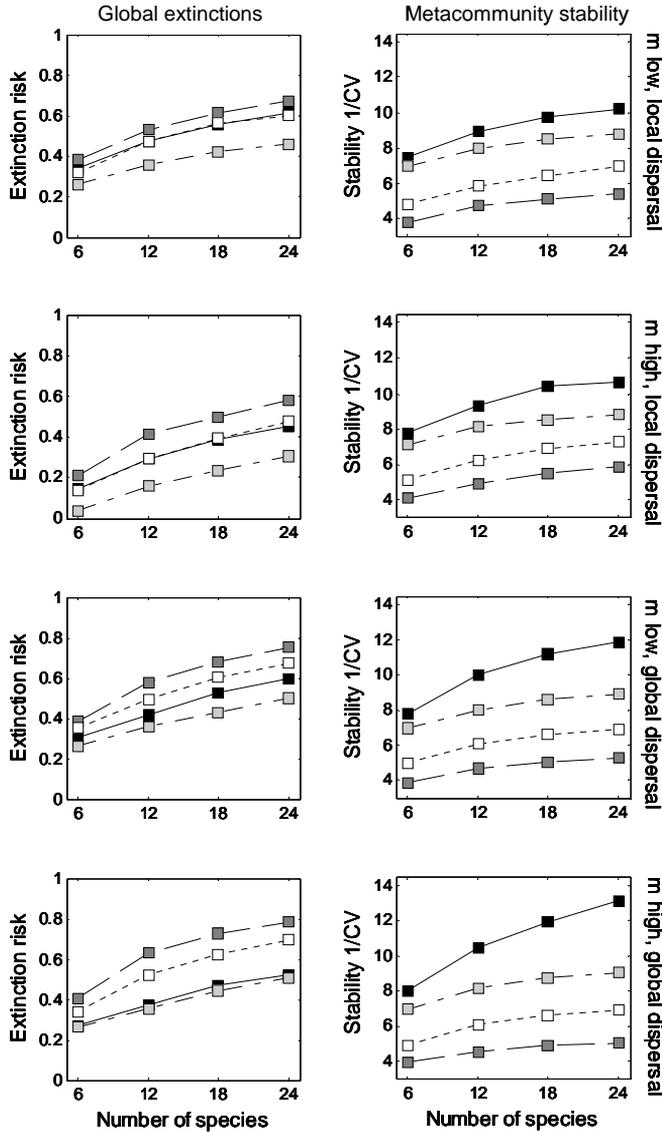
### *Spatial correlation and dispersal patterns*

In metacommunities exposed to environmental variation the spatial processes can affect the dynamics via two pathways: 1) the spatial correlation of each species' response to the environmental variation across patches and 2) via dispersal among patches, where both the rate ( $m$ ) and the strength of the distance dependence is varied (i.e. local or global dispersal). When including a spatial component we still find that the risk of global extinction (Figure 9, left) increases with increasing species richness in the local communities (paper I). A low correlation among species within patches (paper I) and a high correlation among patches increase the risk of species going globally extinct (Figure 1). Our results regarding the correlation among patches are in line with results from other studies showing that synchronous fluctuations of populations across patches will increase the risk of global extinctions (Hudson et al. 1999, Abbott 2011). Species dispersal pattern also has significant effects on the risk of global extinctions; the risk of species going globally extinct is higher when dispersal is global (Figure 1, left, bottom two rows) compared to when dispersal is local (Figure 9, left, top two rows).

The most likely reason for this is that a global dispersal pattern will increase the synchrony among local populations in the landscape (paper III; see also (Eklöf & Ebenman 2006, Mouquet & Loreau 2003). On the other hand, a high rate of migration in combination with localized dispersal increases the frequency of recolonisations and also increases the potential for rescue effects to act (Brown et al. 1977). As a consequence the risk of global extinction cascades decreases.

We found that the pattern of synchrony of species per capita growth rates among patches did not only to depend on the spatial correlation in the environmental variation ('Moran effect') but also on the dispersal rate and dispersal pattern of species. Global dispersal and high rates of migration increase the synchrony (Paper III). Here we found that the "Moran effect" is involved in synchronising the dynamics of the populations across space, but that the strength of this effect is modulated both by the migration rate (Lande et al. 1999, Ranta et al. 1998, Bjørnstad et al. 1999, Liebhold et al. 2004, Goldwyn et al. 2008) and the dispersal pattern of species (Heino et al. 1997). This joint synchronising effect of global dispersal and spatial correlation in the environmental variation can be detrimental for the long-term persistence of species in metacommunities.

The temporal variability in population and community abundances provides an additional measure of stability. In a metacommunity the aggregated stability of primary producers can be measured at the scale of the metapopulation, the local community and the metacommunity as a whole. The effects of species richness on temporal stability can differ among these different scales (France & Duffy 2006).



**Figure 9.** Global extinction risk (left column), and temporal stability,  $1/CV$ , of aggregated abundance of primary producer species in the entire metacommunity (right column) in 10-patch metacommunities as a function of species number in local food webs and the degree of correlation in species response to the environmental variation both within patches and between patches ( $\rho = [Species / Spatial]$ ). The rows in the figure correspond to different species dispersal patterns: the top two rows show results for localized dispersal (low  $c$ ) with low and high migration rate,  $m$ ; the bottom two rows show results for global dispersal (high  $c$ ) with low and high migration rate,  $m$ . Each data point is an average of 200 replicate metacommunities. Error bars (sometimes not visible) show the standard error.

We found that metapopulation stability (stability of the aggregated abundances of all local populations of a species) decreases with increasing spatial correlation and increasing species richness in the local communities (paper III). Similarly, the persistence of species decreases (i.e., the risk of global extinction increases) with increasing spatial correlation and increasing number of species (Figure 9, left). The stability of the aggregate abundance of primary producers at each local community increases with increasing species number and decreasing degree of correlation among species (paper III) which is in line with our results from paper I and other studies of single isolated communities (Yachi & Loreau 1999, Elmqvist et al. 2003).

The temporal stability of the aggregate abundance of all primary producer species in the metacommunity as a whole increases with decreasing spatial correlation and increasing species number within the local communities (Figure 9, right). Recent theoretical work by Loreau & Mouquet (2003) also reported a stabilizing effect of biodiversity on metacommunity stability. Their study deals with competitive communities (communities with a single trophic level) where species were unable to coexist within local communities in the absence of dispersal. Also they assumed that the environmental fluctuations across the landscape were completely asynchronous and there was no functional complementarity among species within local communities (i.e. high correlation among species) (Loreau et al. 2003). We find that functional complementarity (low correlation among species within local communities) increases the metacommunity stability when the spatial correlation is low (Figure 9, right). In the case of asynchrony among species within patches and among populations across patches, a high migration rate in combination with a global dispersal pattern further increased the stability at the metacommunity level (Figure 9, right).

As for the case of single closed communities, the effect of species richness on the stability of metacommunities was two-sided: High species richness within local communities' increases the temporal stability at the metacommunity scale but at the same time reduces the probability of long-term coexistence of species within the metacommunities.

### ***Dispersal risk***

Dispersal of species between patches (local communities) leads to recolonizations and the operation of 'rescue' effects. These processes can potentially stop extinction cascades triggered by a local species loss. However, we found that dispersal could not rescue communities from cascading extinctions when dispersal incurred a risk upon the migrants (paper IV). High migration rates in the presence of high mortality during dispersal increases the risk of local extinctions, since more individuals are then affected by the increased mortality. When dispersal was localized this negative effect of dispersal on local species diversity became less severe as the number of habitat patches in the landscape increased. Increasing patch density decreases the average distance between patches and since the risk is proportional to distance travelled the mortality during dispersal decreases. However, when dispersal is global this positive effect of increasing patch density disappears, because the average distance moved by individuals are then not as strongly affected by the patch density. For a given number of patches localized

dispersal has less negative effects on local species diversity than global dispersal, especially when migration rate is high. This result is in line with the findings of earlier theoretical (Mouquet & Loreau 2003), paper III) and empirical work (Kerr et al. 2002). In addition, when dispersal is global more individuals move longer distances and therefore they will experience a higher risk which will reduce their chances of successfully arriving to another suitable patch. The differences between the two dispersal patterns is most pronounced at high migration rates, since the more individuals that migrate the more significant should the pattern of their movements be (paper III- IV).

Top predators were particularly sensitive to changes in the number of habitat patches and dispersal patterns when dispersal imposes a risk. This is in line with the findings of other studies showing that top predators are particularly vulnerable to habitat loss and fragmentation (Holyoak 2000; Layman et al. 2007). The vulnerability of different types of species to changes in the spatial structure of the landscape (number of habitat patches) and dispersal behaviour of species (migration rates and dispersal distance) might also depend on the trophic structure of the local communities (Melian & Bascompte 2002; paper I-II).

Overall, our results suggest that decreasing the mortality risk of dispersing individuals by constructing habitat corridors or by improving the quality of the habitat matrix might greatly increase the robustness of metacommunities to local loss of species by enhancing recolonisations and rescue effects (see Staddon et al. 2010, for a recent experimental study).

### ***Keystone patches***

Recent studies have applied network theory to real ecological communities in fragmented landscapes, using a wide selection of indices to characterise the contribution of individual habitat patches to landscape connectivity (Urban & Keitt 2001; Bodin & Norberg 2007, Estrada & Bodin 2008, Urban & Keitt 2001). Certain patches may be more important than others in upholding the local or global species diversity in a metacommunity and may then be identified by such a network index. We calculated a range of network indices for the patches in a large set of simulated metacommunities. We then deleted patches in order to identify keystone patches. Here keystone patches are those whose loss will lead to high risks of local and global species extinctions in the metacommunity. All of the indices identified the keystone patch quality to a certain degree. Some of the indices were consistently better than the others and the dependence of the keystone quality on these indices was at least two times larger than for the others. The quality identified by the indices was of being more important for upholding local rather than global diversity. Many parameters were varied between the different metacommunities and as a result of this the models for identifying keystone patches yielded small  $R^2$  values and therefore were not proven to be dependable predictors if applied to particular metacommunities.

## ***5. Concluding remarks***

The theoretical studies in the present thesis suggest that species-rich ecological communities might be more prone to extinction cascades when exposed to a highly variable environment than species-poor communities. A low correlation among species in their responses to the environmental variation further increases the risk of extinction cascades. For any given number of species the risk and extent of extinctions cascades depends on the pattern of interactions among species within the communities. Moreover, we find that previous exposure to extinctions might make communities more robust to new disturbances, because extinctions often lead to changes in the trophic structure of the communities in a direction that promote stability.

The spatial dimension has a strong influence on the risks for extinction cascades. High synchrony in the growth rates of populations across the patches in the landscape is often detrimental for species persistence in the metacommunities. Synchronous fluctuations in the environment and global dispersal of species were factors that induced synchrony in population growth rates across the patches and reduced the probability for recolonisations, hence increasing the risk of extinction. Our studies also suggest that the quality of the matrix might be very important for the likelihood of migrants to reach their target patch. A poor habitat quality in the matrix will increase the mortality during dispersal and hence reduce the potential for recolonisations and ‘rescue effects’ to operate. Using spatially and dynamically explicit models we have also investigated the response of metacommunities to the loss of habitat patches and we have taken a first step towards identifying “keystone patches” in the landscape – patches that are critical for upholding species diversity in the metacommunities.

## ***6. Acknowledgements***

First, I would like to thank my supervisor Bo Ebenman, for given me the opportunity to work in this very exciting area of research and for your scientific guidance and encouragement during my time as a PhD-student. I thank my second supervisor Peter Münger for all your help in killing the bugs that have roamed my code from time to time. To all the members in the Theoretical Biology group, thank you so much for all the great scientific discussions and most of all for all the good times we have had, I will miss you all! I would like to send a special thanks to Nina Håkansson, Frida Lögdberg, Åsa Rybo Landelius and Anna Eklöf for always being supporting and most of all for your friendship. Thank you to all the people at the Biology Department, for all the support and fun we have had throughout the years.

To my parents, Tommy and Carina, thank you for always encouraging and believing in me.

Finally, a very special thank to you, Johan. For all your loving support during all these years, now I am finally coming home, I love you.

## 7. References

- ABBOTT, K.C., 2011. A dispersal-induced paradox: synchrony and stability in stochastic metapopulations. *Ecology Letters*, 14, 1158-1169.
- ABBOTT, K.C., 2007. Does the pattern of population synchrony through space reveal if the Moran effect is acting? *Oikos*, 116, 903-912.
- ADLER, P.B. and DRAKE, J.M., 2008. Environmental variation, stochastic extinction, and competitive coexistence. *The American Naturalist*, 172 E186-E195.
- ADLER, P.B., HILLERISLAMBERS, J., KYRIAKIDIS, P.C., GUAN, Q. and LEVINE, J.M., 2006. Climate variability has a stabilizing effect on the coexistence of prairie grasses. *Proceedings of the National Academy of Sciences*, 103, 12793-12798.
- AMARASEKARE, P. and NISBET, R.M., 2001. Spatial heterogeneity, source-sink dynamics, and the local coexistence of competing Species. *American Naturalist*, 158, 572-584; 572.
- AMARASEKARE, P., 2008. Spatial dynamics of foodwebs. *Annual Review of Ecology, Evolution, and Systematics*, 39, 479-500.
- BASCOMPTE, J. and STOUFFER, D.B., 2009. The assembly and disassembly of ecological networks. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364, 1781-1787.
- BENDER, M.A., KNUTSON, T.R., TULEYA, R.E., SIRUTIS, J.J., VECCHI, G.A., GARNER, S.T. and HELD, I.M., 2010. Modeled impact of anthropogenic warming on the frequency of intense atlantic hurricanes. *Science*, 327, 454-458.
- BJØRNSTAD, O.N., IMS, R.A. and LAMBIN, X., 1999. Spatial population dynamics: analyzing patterns and processes of population synchrony. *Trends in Ecology & Evolution*, 14, 427-432.
- BODIN, Ö. and NORBERG, J., 2007. A Network approach for analyzing spatially structured populations in fragmented landscapes. *Landscape Ecology*, 22, 31-44.
- BODIN, Ö. and SAURA, S., 2010. Ranking individual habitat patches as connectivity providers: Integrating network analysis and patch removal experiments. *Ecological Modelling*, 221, 2393-2405.
- BORRVALL, C. and EBENMAN, B., 2008. Biodiversity and persistence of ecological communities in variable environments. *Ecological Complexity*, 5, 99-105.
- BORRVALL, C., EBENMAN, B. and TOMAS JONSSON, T.J., 2000. Biodiversity lessens the risk of cascading extinction in model food webs. *Ecology Letters*, 3, 131-136.
- BOYCE, M.S., HARIDAS, C.V., LEE, C.T. and the NCEAS working group stochastic demography, 2006. Demography in an increasingly variable world. *Trends in Ecology & Evolution*, 21, 141-148.
- BROWN, J.H. and KODRIC-BROWN, A., 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology*, 58, 445-449.
- BURGMER, T. and HILLEBRAND, H., 2011. Temperature mean and variance alter phytoplankton biomass and biodiversity in a long-term microcosm experiment. *Oikos*, 120, 922-933.
- CADOTTE, M.W., 2006. Metacommunity influences on community richness at multiple spatial scales: A microcosm experiment. *Ecology*, 87, 1008-1016.

- CAMACHO, J., GUIMERÀ, R. and NUNES AMARAL, L.A., 2002. Robust patterns in food web structure. *Physical Review Letters*, 88, 228102.
- CASWELL, H., 1978. Predator-mediated coexistence: A nonequilibrium Model. *The American Naturalist*, 112, 127-154.
- CHESSON, P.L. and WARNER, R.R., 1981. Environmental variability promotes coexistence in lottery competitive systems. *The American Naturalist*, 117, 923-943.
- COWEN, R.K., LWIZA, K.M.M., SPONAUGLE, S., PARIS, C.B. and OLSON, D.B., 2000. Connectivity of marine populations: open or closed? *Science*, 287, 857-859.
- CURTSDOTTER, A., BINZER, A., BROSE, U., DE CASTRO, F., EBENMAN, B., EKLÖF, A., RIEDE, J.O., THIERRY, A. and RALL, B.C., 2011. Robustness to secondary extinctions: Comparing trait-based sequential deletions in static and dynamic food webs. *Basic and Applied Ecology*, 12, 571-580.
- DE VISSER, S.N., FREYMAN, B.P. and OLFF, H., 2011. The Serengeti food web: empirical quantification and analysis of topological changes under increasing human impact. *Journal of Animal Ecology*, 80, 484-494.
- DUFFY, P.B. and TEBALDI, C., 2012. Increasing prevalence of extreme summer temperatures in the U.S. *Climatic Change*, 2. - 487.
- DUNNE, J.A. and WILLIAMS, R.J., 2009. Cascading extinctions and community collapse in model food webs. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364, 1711-1723.
- DUNNE, J.A., WILLIAMS, R.J. and MARTINEZ, N.D., 2002a. Food-web structure and network theory: The role of connectance and size. *Proceedings of the National Academy of Sciences*, 99, 12917-12922.
- DUNNE, J.A., WILLIAMS, R.J. and MARTINEZ, N.D., 2002b. Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecology Letters*, 5, 558-567.
- EASTERLING, D.R., MEEHL, G.A., PARMESAN, C., CHANGNON, S.A., KARL, T.R. and MEARN, L.O., 2000. Climate extremes: observations, modeling, and impacts. *Science*, 289, 2068-2074.
- EBENMAN, B., 2011. Response of ecosystems to realistic extinction sequences. *Journal of Animal Ecology*, 80, 307-309.
- EBENMAN, B. and JONSSON, T., 2005. Using community viability analysis to identify fragile systems and keystone species. *Trends in Ecology & Evolution*, 20, 568-575.
- EBENMAN, B., LAW, R. and BORRVAL, C., 2004. Community viability analysis: the response of ecological communities to species loss. *Ecology*, 85, 2591-2600.
- EKLOEF, A. and EBENMAN, B.O., 2006. Species loss and secondary extinctions in simple and complex model communities. *Journal of Animal Ecology*, 75, 239-246.
- ELMQVIST, T., FOLKE, C., NYSTROM, M., PETERSON, G., BENGTSSON, J., WALKER, B. and NORBERG, J., 2003. Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment*, 1, 488-494.
- ESTRADA, E. and BODIN, O., 2008. Using network centrality measures to manage landscape connectivity. *Ecological Applications*, 18 1810-1825.
- FOWLER, M.S., 2010. Extinction cascades and the distribution of species interactions. *Oikos*, 119, 864-873.
- FRANCE, K.E. and DUFFY, J.E., 2006. Diversity and dispersal interactively affect predictability of ecosystem function. *Nature*, 441, 1139-1143.

- FREEMAN, L.C., 1978. Centrality in social networks conceptual clarification. *Social Networks*, 1, 215-239.
- FUSSMANN, G.F. and HEBER, G., 2002. Food web complexity and chaotic population dynamics. *Ecology Letters*, 5, 394-401.
- GAINES, M.S. and MCCLENAGHAN, L.R., JR., 1980. Dispersal in small mammals. *Annual Review of Ecology and Systematics*, 11, 163-196.
- GOLDWYN, E.E. and HASTINGS, A., 2008. When can dispersal synchronize populations? *Theoretical population biology*, 73, 395-402.
- GONZALEZ, A. and LOREAU, M., 2009. The causes and consequences of compensatory dynamics in ecological communities. *Annual Review of Ecology, Evolution, and Systematics*, 40,
- GOUDARD, A. and LOREAU, M., 2008. Nontrophic interactions, biodiversity, and ecosystem functioning: an interaction web model. *The American Naturalist*, 171, 91-106.
- GRAVEL, D., GUICHARD, F. and HOCHBERG, M.E., 2011. Species coexistence in a variable world. *Ecology Letters*, 14, 828-839.
- GRIFFEN, BLAINE D. DRAKE, JOHN M., 2008. A review of extinction in experimental populations. *Journal of Animal Ecology*, 77, 1274-1287.
- GROSS, K. and CARDINALE, B.J., 2005. The functional consequences of random vs. ordered species extinctions. *Ecology Letters*, 8, 409-418.
- GROSS, T., RUDOLF, L., LEVIN, S.A. and DIECKMANN, U., 2009. Generalized models reveal stabilizing factors in food webs. *Science*, 325, 747-750.
- GUIMERÀ, R., STOUFFER, D.B., SALES-PARDO, M., LEICHT, E.A., NEWMAN, M.E.J. and AMARAL, L.A.N., 2010. Origin of compartmentalization in food webs. *Ecology*, 91, 2941-2951.
- HADDAD, N.M., CRUTSINGER, G.M., GROSS, K., HAARSTAD, J. and TILMAN, D., 2011. Plant diversity and the stability of foodwebs. *Ecology Letters*, 14, 42-46.
- HANSKI, I. and WOIWOD, I.P., 1993. Spatial synchrony in the dynamics of moth and aphid populations. *Journal of Animal Ecology*, 62, 656-668.
- HEINO, M., KAITALA, V., RANTA, E. and LINDSTROM, J., 1997. Synchronous dynamics and rates of extinction in spatially structured populations. *Proceedings: Biological Sciences*, 264, 481-486.
- HOLYOAK, M., 2000. Habitat subdivision causes changes in food web structure. *Ecology Letters*, 3, 509-515.
- HOLYOAK, M., LEIBOLD, M.A. and HOLT, R.D., 2005. Metacommunities: spatial dynamics and ecological communities. The University of Chicago Press, Chicago.
- HOLYOAK, M. and LAWLER, S.P., 1996. The role of dispersal in predator-prey metapopulation dynamics. *The Journal of Animal Ecology*, 65, 640-652.
- HUDSON, P.J. and CATTADORI, I.M., 1999. The Moran effect: a cause of population synchrony. *Trends in Ecology & Evolution*, 14, 1-2.
- HUGHES, J.B. and ROUGHGARDEN, J., 2000. Species diversity and biomass stability. *The American Naturalist*, 155, 618-627.
- IMS, R.A. and ANDREASSEN, H.P., 2000. Spatial synchronization of vole population dynamics by predatory birds. *Nature*, 408, 194-196.
- IPPC, INTERGOVERNMENTAL PANEL ON CLIMATE CHANGE, 2007. Climate Change 2007: Synthesis Report.

- IVES, A., KLUG, J. and GROSS, K., 2000. Stability and species richness in complex communities. *Ecology Letters*, 3, 399-411.
- IVES, A.R. and CARDINALE, B.J., 2004. Food-web interactions govern the resistance of communities after non-random extinctions. *Nature*, 429, 174-177.
- IVES, A.R. and CARPENTER, S.R., 2007. Stability and diversity of ecosystems. *Science*, 317, 58-62.
- JENTSCH, A., KREYLING, J. and BEIERKUHNLEIN, C., 2007. A new generation of climate-change experiments: events, not trends. *Frontiers in Ecology and the Environment*, 5, 365-374.
- JIANG, L. and PU, Z., 2009. Different effects of species diversity on temporal stability in single-trophic and multitrophic communities. *The American Naturalist*, 174, 651-659.
- JULIA J.F.G. HUNT, M.B.B., 2009. The effects of colonization, extinction and competition on co-existence in metacommunities. *Journal of Animal Ecology*, 78, 866-879.
- KERR, B., RILEY, M.A., FELDMAN, M.W. and BOHANNAN, B.J.M., 2002. Local dispersal promotes biodiversity in a real-life game of rock-paper-scissors. *Nature*, 418, 171-174.
- KNEITEL, J. and MILLER, T., 2003. Dispersal rates affect species composition in metacommunities of *Sarracenia purpurea* inquilines. *The American Naturalist*, 162, 165-171.
- KOKKORIS, G.D., TROUMBIS, A.Y. and LAWTON, J.H., 1999. Patterns of species interaction strength in assembled theoretical competition communities. *Ecology Letters*, 2, 70-74.
- KOKKORIS, G.D., JANSEN, V.A.A., LOREAU, M. and TROUMBIS, A.Y., 2002. Variability in interaction strength and implications for biodiversity. *Journal of Animal Ecology*, 71, 362-371.
- KONDOH, M., 2008. Building trophic modules into a persistent food web. *Proceedings of the National Academy of Sciences*, 105, 16631-16635.
- LANDE, R., ENGEN, S. and SÆTHER, B., 1999. Spatial scale of population synchrony: environmental correlation versus dispersal and density regulation. *The American Naturalist*, 154, 271-281.
- LAYMAN, C.A., QUATTROCHI, J.P., PEYER, C.M. and ALLGEIER, J.E., 2007. Niche width collapse in a resilient top predator following ecosystem fragmentation. *Ecology Letters*, 10, 937-944.
- LEHMAN, C. and TILMAN, D., 2000. Biodiversity, stability, and productivity in competitive communities. *The American Naturalist*, 156, 534-552.
- LEIBOLD, M.A., HOLYOAK, M., MOUQUET, N., AMARASEKARE, P., CHASE, J.M., HOOPES, M.F., HOLT, R.D., SHURIN, J.B., LAW, R., TILMAN, D., LOREAU, M. and GONZALEZ, A., 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters*, 7, 601-613.
- LEVIN, S.A., 1974. Dispersion and population interactions. *The American Naturalist*, 108, 207-228.
- LIEBHOLD, A., KOENIG, W.D. and BJORNSTAD, O.N., 2004. Spatial synchrony in population dynamics. *Annual Review of Ecology, Evolution, and Systematics*, 35, 467-490.

- LINDSTRÖM, T., HÅKANSSON, N., WESTERBERG, L. and WENNERGREN, U., 2008. Splitting the tail of the displacement kernel shows the unimportance of kurtosis. *Ecology*, 89, 1784-1790.
- LÖGDBERG, F. and WENNERGREN, U., 2012. Spectral color, synchrony, and extinction risk. *Theoretical Ecology*. DOI:10.1007/s12080-011-0145-x
- LOREAU, M. and DE MAZANCOURT, C., 2008. Species synchrony and its drivers: neutral and nonneutral community dynamics in fluctuating environments. *The American Naturalist*, 172, E48-E66.
- LOREAU, M., MOUQUET, N. and GONZALEZ, A., 2003. Biodiversity as spatial insurance in heterogeneous landscapes. *Proceedings of the National Academy of Sciences*, 100, 12765-12770.
- MACARTHUR, R., 1955. Fluctuations of animal populations and a measure of community stability. *Ecology*, 36, 533-536.
- MACARTHUR, R.H., DIAMOND, J.M. and KARR, J.R., 1972. Density compensation in island faunas. *Ecology*, 53, 330-342.
- MAY, R.M., 1973a. Stability and complexity in model ecosystems. 1 st edn.: Princeton University Press, Princeton, New Jersey.
- MAY, R.M., 1973b. Stability in randomly fluctuating versus deterministic environments. *The American Naturalist*, 107, 621-650.
- MCCANN, K.S., 2000. The diversity-stability debate. *Nature*, 405, 228-233.
- MCCANN, K. and HASTINGS, A., 1997. Re-evaluating the omnivory-stability relationship in food webs. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 264, 1249-1254.
- MEEHL, G.A. and TEBALDI, C., 2004. More intense, more frequent, and longer lasting heat waves in the 21st century. *Science*, 305, 994-997.
- MELIÁN, C.J. and BASCOMPTE, J., 2002. Complex networks: two ways to be robust? *Ecology Letters*, 5, 705-708.
- MELIÁN, C.J. and BASCOMPTE, J., 2002. Food web structure and habitat loss. *Ecology Letters*, 5, 37-46.
- MILLER, A.D., ROXBURGH, S.H. and SHEA, K., 2011. How frequency and intensity shape diversity-disturbance relationships. *Proceedings of the National Academy of Sciences*, 108, 5643-5648.
- MILO, R., SHEN-ORR, S., ITZKOVITZ, S., KASHTAN, N., CHKLOVSKII, D. and ALON, U., 2002. Network motifs: simple building blocks of complex networks. *Science*, 298, 824-827.
- MIN, S., ZHANG, X., ZWIERS, F.W. and HEGERL, G.C., 2011. Human contribution to more-intense precipitation extremes. *Nature*, 470, 378-381.
- MINOR, E.S. and URBAN, D.L., 2007. Graph theory as a proxy for spatially explicit population models in conservation planning. *Ecological Applications*, 17, 1771-1782.
- MONTOYA, J.M., PIMM, S.L. and SOLE, R.V., 2006. Ecological networks and their fragility. *Nature*, 442, 259-264.
- MORAN, P.A.P., 1953. The statistical analysis of the canadian lynx cycle. 1. Structure and prediction. *Australian Journal of Zoology*, 1, 163-173.
- MORRIS, W.F., PFISTER, C.A., TULJAPURKAR, S., HARIDAS, C.V., BOGGS, C.L.,

- BOYCE, M.S., BRUNA, E.M., CHURCH, D.R., COULSON, T., DOAK, D.F., FORSYTH, S., GAILLARD, J., HORVITZ, C.C., KALISZ, S., KENDALL, B.E., KNIGHT, T.M., LEE, C.T. and MENGES, E.S., 2008. Longevity can buffer plant and animal populations against changing climatic variability. *Ecology*, 89, 19-25.
- MOUQUET, N. and LOREAU, M., 2002. Coexistence in metacommunities: the regional similarity hypothesis. *American Naturalist*, 159, 420-426.
- MOUQUET, N. and LOREAU, M., 2003. Community patterns in source-sink metacommunities. *The American Naturalist*, 162, 544-557.
- NATHAN, R., SCHURR, F.M., SPIEGEL, O., STEINITZ, O., TRAKHTENBROT, A. and TSOAR, A., 2008. Mechanisms of long-distance seed dispersal. *Trends in Ecology & Evolution*, 23, 638-647.
- OTTO, S.B., RALL, B.C. and BROSE, U., 2007. Allometric degree distributions facilitate food-web stability. *Nature*, 450, 1226-1229.
- PEREIRA, H.M., LEADLEY, P.W., PROENÇA, V., ALKEMADE, R., SCHARLEMANN, J.P.W., FERNANDEZ-MANJARRÉS, J.F., ARAÚJO, M.B., BALVANERA, P., BIGGS, R., CHEUNG, W.W.L., CHINI, L., COOPER, H.D., GILMAN, E.L., GUÉNETTE, S., HURTT, G.C., HUNTINGTON, H.P., MACE, G.M., OBERDORFF, T., REVENGA, C., RODRIGUES, P., SCHOLES, R.J., SUMAILA, U.R. and WALPOLE, M., 2010. Scenarios for global biodiversity in the 21st century. *Science*, 330, 1496-1501.
- PETCHEY, O.L., 2000. Prey diversity, prey composition, and predator population dynamics in experimental microcosms. *Journal of Animal Ecology*, 69, 874-882.
- PETCHEY, O.L., EKLOEF, A., BORRVALL, C. and EBENMAN, B.O., 2008. Trophically Unique Species Are Vulnerable to Cascading Extinction. *The American Naturalist*, 171, 568-579.
- PIMM, S.L., 1980. Food web design and the effect of species deletion. *Oikos*, 35, 139-149.
- PIMM, S.L. and LAWTON, J.H., 1980. Are food webs divided into compartments? *Journal of Animal Ecology*, 49, 879-898.
- PIMM, S.L. and RAVEN, P., 2000. Biodiversity: extinction by numbers. *Nature*, 403, 843-845.
- RANTA, E., KAITALA, V. and LUNDBERG, P., 1998. Population variability in space and time: the dynamics of synchronous population fluctuations. *Oikos*, 83, 376-382.
- RIPA, J. and LUNDBERG, P., 1996. Noise colour and the risk of population extinctions. *Proceedings: Biological Sciences*, 263, 1751-1753.
- ROONEY, N., MCCANN, K.S. and MOORE, J.C., 2008. A landscape theory for food web architecture. *Ecology Letters*, 11, 867-881.
- ROSCHE, C., WEIGELT, A., PROULX, R., MARQUARD, E., SCHUMACHER, J., WEISSER, W.W. and SCHMID, B., 2011. Identifying population- and community-level mechanisms of diversity? Stability relationships in experimental grasslands. *Journal of Ecology*, 99, 1460-1469.
- ROSENZWEIG, M.L. and MACARTHUR, R.H., 1963. Graphical representation and stability conditions of predator-prey interactions. *The American Naturalist*, 97, 209-223.
- RUOKOLAINEN, L. and FOWLER, M.S., 2008. Community extinction patterns in

- coloured environments. *Proceedings of the Royal Society B: Biological Sciences*, 275, 1775-1783.
- RUOKOLAINEN, L., FOWLER, M.S. and RANTA, E., 2007. Extinctions in competitive communities forced by coloured environmental variation. *Oikos*, 116, 439-448.
- RUOKOLAINEN, L., LINDÉN, A., KAITALA, V. and FOWLER, M.S., 2009. Ecological and evolutionary dynamics under coloured environmental variation. *Trends in Ecology & Evolution*, 24, 555-563.
- RUXTON, G.D., GONZALEZ-ANDUJAR, J.L. and PERRY, J.N., 1997. Mortality During Dispersal and the Stability of a Metapopulation. *Journal of theoretical biology*, 186, 389-396.
- SAAVEDRA, S., REED-TSOCHAS, F. and UZZI, B., 2008. Asymmetric disassembly and robustness in declining networks. *Proceedings of the National Academy of Sciences*, 105, 16466-16471.
- SAURA, S. and PASCUAL-HORTAL, L., 2007. A new habitat availability index to integrate connectivity in landscape conservation planning: Comparison with existing indices and application to a case study. *Landscape and Urban Planning*, 83, 91-103.
- SHURIN, J.B., WINDER, M., ADRIAN, R., KELLER, W., MATTHEWS, B., PATERSON, A.M. *et al.* (2010). Environmental stability and lake zooplankton diversity – contrasting effects of chemical and thermal variability. *Ecology Letters*, 13, 453-463.
- SMALL, R.J., MARCSTRÖM, Y. and WILLEBRAND, T., 1993. Synchronous and nonsynchronous population fluctuations of some predators and their prey in central Sweden. *Ecography*, 16, 360-364.
- SOLÉ, R.V. and MONTÓYA, M., 2001. Complexity and fragility in ecological networks. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 268, 2039-2045.
- SRINIVASAN, U.T., DUNNE, J.A., HARTE, J. and MARTINEZ, N.D., 2007. Response of complex food webs to realistic extinction sequences. *Ecology*, 88, 671-682.
- STADDON, P., LINDO, Z., CRITTENDEN, P.D., GILBERT, F. and GONZALEZ, A. 2010. Connectivity, non-random extinction and ecosystem function in experimental metacommunities. *Ecology Letters*, 13, 543-552.
- STOUFFER, D.B., CAMACHO, J., GUIMERÀ, R., NG, C.A. and NUNES AMARAL, L.A., 2005. Quantitative patterns in the structure of model and empirical food webs. *Ecology*, 86, 1301-1311.
- STOUFFER, D.B. and BASCOMPTE, J., 2011. Compartmentalization increases food-web persistence. *Proceedings of the National Academy of Sciences*, 108, 3648-3652.
- STOUFFER, D.B. and BASCOMPTE, J., 2010. Understanding food-web persistence from local to global scales. *Ecology Letters*, 13, 154-161.
- STOUFFER, D.B., CAMACHO, J., JIANG, W. and NUNES AMARAL, L.A., 2007. Evidence for the existence of a robust pattern of prey selection in food webs. *Proceedings of the Royal Society B: Biological Sciences*, 274, 1931-1940.
- STROGATZ, S.H., 2001. Exploring complex networks. *Nature*, 410, 268-276.
- THEBAULT, E. and FONTAINE, C., 2010. Stability of ecological communities and the

- architecture of mutualistic and trophic networks. *Science*, 329, 853-856.
- THEBAULT, E. and LOREAU, M., 2005. Trophic interactions and the relationship between species diversity and ecosystem stability. *The American Naturalist*, 166, E95-E114.
- TILMAN, D., 1996. Biodiversity: population versus ecosystem stability. *Ecology*, 77, 350-363.
- URBAN, D. and KEITT, T., 2001. Landscape connectivity: A graph-theoretic perspective. *Ecology*, 82, 1205-1218.
- WILSON, D.S., 1992. Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. *Ecology*, 73, 1984-2000.
- YACHI, S. and LOREAU, M., 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proceedings of the National Academy of Sciences*, 96, 1463-1468.