The Big Picture from Small Landscapes

Investigations of Spatial Patterns and Processes using a Model Metacommunity

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Abstract

Habitat fragmentation is a major current threat to natural environments. Still, fundamental questions of what influences ecological communities in spatially structured habitats are unanswered. In this thesis, microarthropods in moss patches were used in a model system, where both biotic and abiotic factors could be manipulated. In four studies, I investigated how isolation distance, connectivity, habitat size, dispersal barriers, matrix quality, and environmental quality influenced the occurrence, abundance and diversity of mites (Acari), and springtails (Collembola). First, I show that the effects of habitat fragmentation was profound and species specific. Inter-patch dispersal between isolated patches was low in natural settings compared to mainland-island dispersal, and populations in the mainland had a large influence even on distant communities. Secondly, I show that connecting fragmented patches by habitat corridors increased the dispersal throughout the landscape, but that this had complex and unpredictable results. Habitat corridors interacted with the surrounding matrix which led to counterintuitive patterns. For predatory mites and collembolans, habitat corridors had a negative impact when the corridors intersected a matrix of poor quality, severely reducing their abundance, probably due to increased edge effects. Moreover, oribatid mites decreased in landscapes with corridors, likely due to increased predation, caused by increased connectivity, favoring predators. Thirdly, I show that community assembly following a disturbance event was predictable, based on random colonization of individuals from the surrounding pool of individuals. In contrast, community disassembly following habitat fragmentation was highly unpredictable, and could not be explained by a random loss of individuals. The fourth study examined natural situations and show that while the spatial factors connectivity and distance had a lasting influence on local communities, habitat area was the major determining factor for both density and species richness.

Keywords: Metacommunity ecology, Fragmentation, Dispersal, Connectivity, Disturbance, Microarthropods, Acari, Collembola, Oribatida

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"This was what was keeping me awake at night," Walter said. "This fragmentation."

Walter Berglund in *Freedom*, by Jonathan Franzen

Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Jens Åström and Jan Bengtsson (2011). Patch size matters more than dispersal distance in a mainland-island metacommunity. *Oecologia* (in press). DOI: 10.1007/s00442-011-2024-y

II Jens Åström and Tomas Pärt. Matrix quality and trophic interactions determine response to corridors in an experimental metacommunity. (manuscript).

III Jens Åström. Predictable community assembly and unpredictable disassembly in a spatially structured landscape. (manuscript).

IV Jens Åström, Niklas Lindberg and Jan Bengtsson. Lasting influence of space and environment on community composition in a naturally fragmented moss patch ecosystem. (manuscript).

Paper I is reproduced with permission from Springer. The final publication will be available at www.springerlink.com.

The contribution of Jens Åström to the papers included in this thesis was as follows:

I Main author, practical work, identification, and analysis. Experimental design and idea together with Jan Bengtsson. Co-author: Jan Bengtsson.

II Main author, design, practical work, and analysis. Co-author: Tomas Pärt.

III Author, design, practical work, and analysis.

IV Main author and analysis. Design by Jan Bengtsson and Niklas Lindberg. Field work and identification by Niklas Lindberg. Co-authors: Jan Bengtsson and Niklas Lindberg.

1 Introduction

The destruction and alteration of habitat has had the largest influence to date on the natural environment, and still is considered by many ecologists to be the most pressing problem, despite the enormous attention of climate change in recent years. It is estimated that between 20 and 70% of the potential area of the world's different biomes have been converted from their natural state, primarily to agriculture, with the exception of boreal forests and tundra (Millenium Ecosystem Assessment, 2005). Current trends in population and economic growth suggest that the anthropogenic influence will continue to increase (see e.g. McKee et al., 2004). In addition to the sheer disappearance of habitat, there is also a consistent trend of increased habitat fragmentation. Habitat fragmentation is defined as the breaking up of habitat into smaller pieces, but typically entails both loss of habitat, decreased connectivity, and increased isolation distance between habitat patches (Wilcox and Murphy, 1985; Fahrig, 2003; Lindenmayer and Fischer, 2006; Fletcher et al., 2007). Understanding how habitat fragmentation influences ecosystems remains a central task in ecology. The influences of habitat fragmentation is of interest not only to applied but also to basic ecology. Many pristine ecosystems are naturally fragmented and understanding how fragmentation affects these system is necessary for understanding the system as a whole. It is a patchy world, and we ought to know what that means.

The effects of fragmentation on animal communities is a central theme in this thesis. This includes habitat loss, loss of connectivity, and increased isolation distance. In addition, I explore the importance of the explanatory factors disturbance and environmental quality. I use a spatially structured terrestrial model system to investigate patterns of the response variables abundance, diversity, and community composition. The main processes of importance are dispersal, colonization, extinction, competition, and predation. Figure 1 shows some of the terms that are central in this thesis.

Dispersal, environmental heterogeneity, dynamics, and disturbance are main factors of interest to ecology, in any fragmented ecosystem, as they have a determining influence on abundance, diversity, and species composition (Hanski, 1999; Holyoak et al., 2005). If there is no dispersal whatsoever, each habitat patch is isolated and could just as well be investigated separately. If there is extremely high dispersal, habitat patches will have equal communities and the system might as well be analyzed as one unit. But many fragmented systems have intermediate dispersal rates and the details of dispersal will influence local as well as regional abundance and composition. For instance, species specific dispersal rates can greatly influence

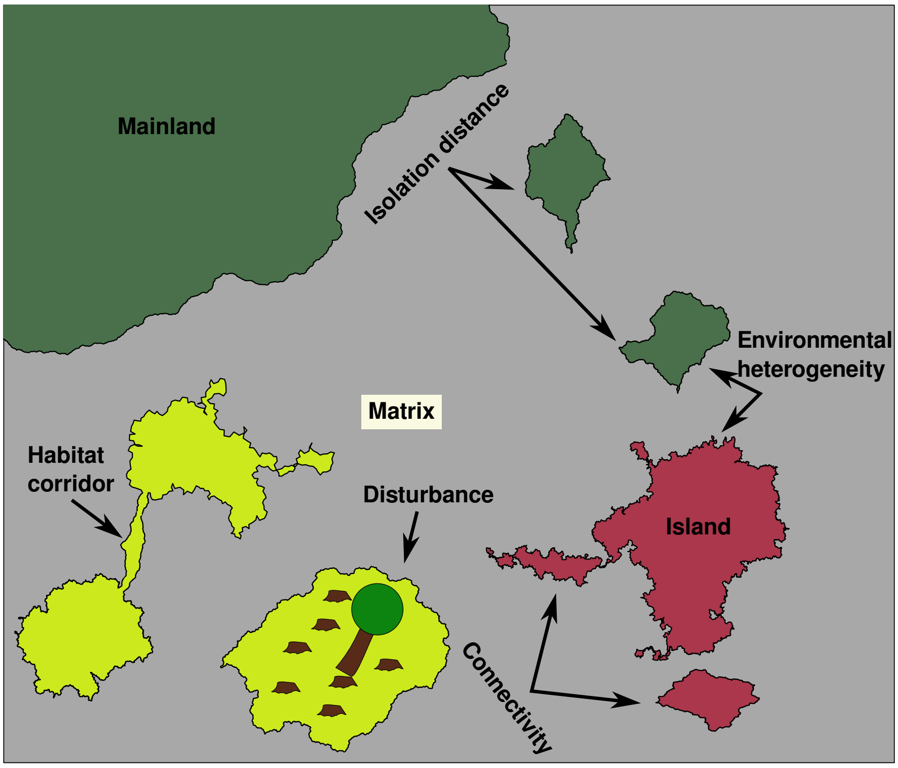


Figure 1: Illustration of some landscape terms used in this thesis.

community composition (Tilman, 1994).

Dispersal between fragmented patches acts as a homogenizing force, evening out transient differences between communities. The frequency and size of local disturbances or local population dynamics will determine to what extent differences between patches are reconstructed. If there are no local dynamics or disturbances, all patches will eventually be identical, barring lasting differences in environmental quality. The response to disturbance or the strength of local population dynamics is therefore a key influencing factor of spatially structured communities.

Lastly, environmental differences will determine lasting differences between individual habitat patches. The influence of environmental heterogeneity is therefore another key factor in spatially structured landscapes (Cottenie, 2005). Effects of dispersal and disturbance on abundance and diversity was investigated in article I.

The most commonly reported consequence of habitat fragmentation is decreased abundances and diversity (Fahrig, 2003). In addition, depending on whether certain species, or groups of species with certain qualities, are more sensitive to habitat fragmentation, fragmentation can alter the composition and functioning of communities, and in turn affect the ability of ecosystems to provide ecosystem services (Ostfeld and LoGiudice, 2003; Tscharntke et al., 2005; Klein et al., 2007). Species specific responses are therefore of interest when predicting the effects of current and future fragmentation.

A common measure to combat the negative effects of fragmentation is increasing connectivity by forming habitat corridors, or planning e.g. forest management such that strips of habitat remain between larger patches of undisturbed forest (see e.g. Beier and Noss, 1998, and following discussion). The basic idea is to increase the effective home ranges of the animals, and increase dispersal, which may lead to decreased species loss by so called "rescue effects" (Brown and Kodric-Brown, 1977) and recolonizations after local extinctions. Rescue effects is the subsidizing of local patches by inter-patch dispersal, and require three things. First, local populations must occasionally be small enough to show increases by inter-patch dispersal. Second, population dynamics must be asynchronous so that temporary low abundance in one patch can be compensated by an excess in another patch. Thirdly, the corridors must represent a large enough improvement in dispersal conditions compared to dispersal through the surrounding matrix. The potential for rescue effects or recolonizations through corridors was investigated in article II. There, I manipulated connectivity and matrix quality to test requisite three, and manipulated environmental stress to test requisites one and two.

But responses to habitat fragmentation need not be negative for all species. Some species may capitalize on, for example, the increased edge to area ratio of smaller habitats, which may influence the microclimate (Kremsater and Bunnell, 1999). Nest predators may also have better luck finding birds' nests in fragmented landscapes, naturally to the detriment of the predated bird species (Chalfoun et al., 2002). Habitat fragmentation may also lead to decreased predation pressure (Simberloff and Cox, 1987) since many predators require larger home ranges than their prey. All in all, species react differently to changes of spatial structure. This may manifest both as differences of how communities disassemble (how habitats lose species), and of how communities assemble (how habitats are colonized). Effects on community disassembly vs assembly processes were investigated in article III.

Articles I-III cover time scales that represents zero to a few generations of the study organisms, and are therefore subject to possible transient dynamics. The factors that influence communities on shorter time scales might be different than those that matter on equilibrium time scales. The relevance of these results may therefore be conditional on the time scale that is used. The lasting influences of connectivity, isolation distance, habitat size, and environmental factors on abundance, diversity, and community composition were investigated in article IV.

2 Background

What does moss on a roof have to do with the largest current environmental problem? It does seem a bit odd when you think about it. But such miniature landscapes may not be so obscure and irrelevant as they first seem. If fragmentation experiments with a bryophyte-microarthropod model system is a leaf on a small branch, time then to roughly sketch the tree trunk it is connected to.

2.1 Ecology

A large portion of ecology is occupied with understanding and describing the presence and abundance of organisms. Why is this species here and not there? Why is this species more abundant in a specific locality than in others? These questions are so central in ecology that it is sometimes cited as the definition of the whole scientific field (Andrewartha and Birch, 1986). It is central not only because of its generality, but also because of its applicability. This is because the answer to what determines the presence and abundance of organisms entails the answer to more pertinent questions: "What will happen to this species if we manipulate its environment in a certain way?", "What should we do if we want this species here?" and "What will happen if this species is not here?". Knowledge of what determines presence and abundances of organisms is simply the basis of any action to manage or conserve them.

Traditionally, a lot of attention has been given to the influence of environmental factors on community composition (Hutchinson, 1957; Whittaker, 1975). Through the years, environmental constraints have been seen as the main determinant of species distributions, event to the point that each set of environmental qualities defined a climax community which was the deterministic end point of succession (Clements, 1916). Disturbance events could temporarily cause local populations to diverge from the path, but the final community was always set by the environmental characteristics of each locality.

But few species are islands, although they may live on them, and it is important to acknowledge species interactions. Species are seldom isolated enough that we can completely disregard the species that surround them. Populations of species live in communities, and therefore a large branch of the tree of ecology is community ecology.

2.2 Community ecology

Community ecology emphasizes the interplay between populations of different species. By this, the community ecology version of the question "Why is this organism here?" becomes "How do the interactions between populations affect the presence of this organism?". This question can be quite complex, since a multitude of interactions are possible and often co-occur. Examples include competition, where one or more species experience negative consequences by the presence of another species, predation, where one organism is the food source of another, and various forms of facilitation where one or more species benefit from the presence of another species without harming that species.

Community ecology addresses the differences between species, but is also occupied with similarities. The general prediction is that similar species cannot co-occur indefinately (Hardin, 1960; Chesson, 2000). In the absence of complicating features, one species will invariably outcompete the other, creating an overall equilibrium of species richness. Skepticism of the competitive equilibrium have been around for a long time (Huston, 1979). Still, the idea of competitive exclusion has caused some bewilderment, particularly in soil ecology, which can be of relevance for this thesis since the model system used is partly a soil system. Soils commonly display impressive biodiversity in small areas despite a seeming similarity between species (Anderson, 1975). The conventional prerequisite for high biodiversity is that the environment and surrounding species must provide a setting where differences between species can be expressed. For instance, species may differ in their response to disturbance, spatial distance between resources, in their ability to utilize certain refugi,a or in their reactions to an environmental stressor (Chesson, 2000). A habitat that provides heterogeneity in these respects is therefore predicted to harbor more species than a habitat that is homogeneous in these regards. Here also lies one possible explanation to the high diversity of many soil communities, soils may be more heterogeneous at the scale of their inhabiting organisms than larger habitats, and soil organisms may also not be so similar as they might seem and may display intricate interactions (Giller, 1996; Wardle, 2006).

The classical theories that names the environment as the main deter-

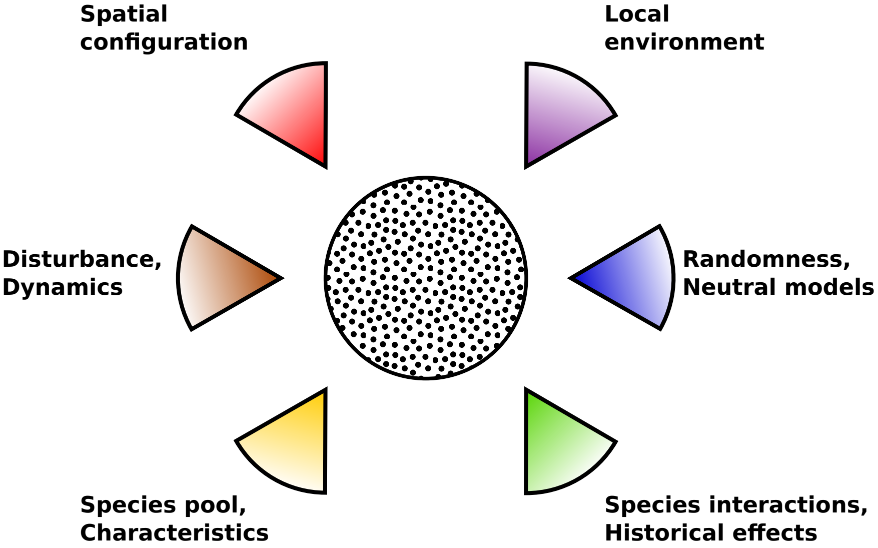


Figure 2: List of factors that together determine community composition. Article I mainly focuses on spatial configuration and disturbance but show the influence of species identities as well. Article II explores spatial configuration, disturbance, species interactions, and some aspects of the local environment. Article III deal with spatial configuration, disturbance, species pool, historical effects, and randomness. Article IV explores the relative role of spatial configuration, environmental constraints, and randomness.

minant of the composition of communities (e.g. Hutchinson, 1957) fails to capture much of the interesting variability in natural communities, and models highlighting the dispersal of individuals have long since started to play a larger role. In the 1960s, Macarthur and Wilson developed the theory of island-biogeography which models the species richness of islands as the equilibrium between immigration, emigration, and extinction events (MacArthur and Wilson, 1963, 1967). The theory is still central in modern ecology as it can be applied to any habitat surrounded by a distinctly different habitat. This theory postulates that immigration is negatively affected by increased distance from dispersal sources and that extinction rates increase with decreased habitat size. The species richness of an island or any fragmented habitat could thereby in theory be predicted, by knowing the habitat size and distance to the dispersal source. Amendments to the theory include increased colonization rates to larger islands due to their larger "target size" (Lomolino, 1990), disturbance rates that are influenced by habitat size (Schoener et al., 2001; Jonsson et al., 2009), and the possibility for preempting extinctions by between island dispersal, so called "rescue effects" (Brown and Kodric-Brown, 1977).

By the 1970s, the focus on deterministic outcomes and equilibrium states of communitites gave way to theories that better captured the dynamics of populations. Robert May showed that many populations are inherently unpredictable in that small changes in initial states can lead to wildly different outcomes (May, 1974). Complex species interactions can also significantly determine community composition, which may, to some extent, be determined by chance events (Pimm, 1991; Law and Leibold, 2005). Such effects include priority effects where an early colonizer can monopolize a resource and hinder subsequent colonizations by other species (see e.g. Blaustein and Margalit, 1996; Almany, 2003), and cases of facilitation where certain species require the presence of other species (Siles et al., 2010).

From this broad introduction, it is clear that community ecologists have to consider a large set of determining factors if they whish to explain and predict community composition. Figure 2 lists different determining factors and how they are addressed in this thesis.

Although diversity and abundance patterns in community ecology have been linked to spatial factors, such as habitat size and edge to area ratios, the focus has traditionally been on one community at a time. But just as species seldom are islands, communities are seldom islands (although communities on islands make interesting study objects). Communities frequently interact with each other, by dispersal of individuals between them. This has led ecologists to increasingly target sets of communities, or metacommunities in their research.

2.3 Metacommunity ecology

Metacommunity theory (Leibold et al., 2004; Holyoak et al., 2005) has many of its roots in metapopulation theory where populations in separate habitats interact by dispersal, collectively constituting a higher level metapopulation (Hanski, 1999). But while this theory deals with one species at a time, metacommunity theory incorporates multiple species or entire communities. At the current state, metacommunity theory is an ambitious field but with somewhat vague predictions. It sets out to unify several different types of processes and seemingly different types of communities under a common framework. Four conceptual perspectives, or concepts, of what

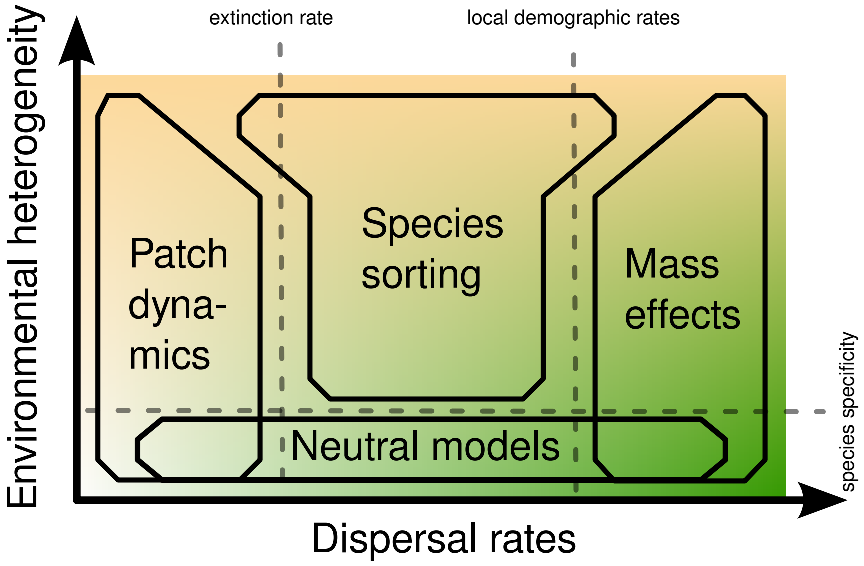


Figure 3: Schematic representation of the four metacommunity concepts. Patch dynamics occur when dispersal rates are low in relation to local extinction rates so that some potentially suitable patches are unoccupied. Mass effects occur when dispersal rates are higher than local demographic rates so that dispersing individuals influence abundance and not only occurrence. Species sorting refers to when occurrence and abundance foremost is determined by environmental qualities or species interaction so that species are sorted into suitable habitats. It is particularly important at intermediate dispersal rates and require environmental heterogeneity above and beyond the sometimes species specific sensitivities to this variation. Neutral models refer to when species effectively have similar fitness in relation to the heterogeneity of environment or species interactions that is present. Adapted after original idea by Matthew Leibold (Metacommunity workshop, 2008).

governs ecological communities are often cited as a main outcome of metacommunity theory; patch dynamics, species sorting, mass effects, and the neutral perspective (Chase et al., 2005). Still, the classification of communities according to these four boxes is neither straightforward, nor necessarily the end goal. Nevertheless, these four perspectives are helpful analytical tools for understanding how a community is related to two key factors: environmental heterogeneity and dispersal rates. Figure 3 is a schematic representation of how the four concepts patch dynamics, species sorting, mass effects, and neutral models can be thought to relate to each other, although it should be mentioned that it does not reflect a scientific consensus.

In patch dynamic systems, dispersal is low enough that local extinctions are not immediately compensated by colonizations. Some potentially suitable patches are therefore empty simply because they have not yet been colonized. Regional diversity and abundance is maintained at the equilibrium between colonizations and extinctions, similar to classical metapopulation theory (Levins, 1969; Hanski, 1999). At any given moment, local presence will thus be governed to a high degree by chance events.

In species sorting systems, occurrence and abundance is mainly determined by the interactions between an organism and its environment or between different species. The importance of species sorting will therefore increase with increased heterogeneity and range of differences in the environment and species interactions. Species sorting has its dominating place at intermediate dispersal rates. Dispersal rates have to be high enough that species with special affinity to a certain environment can find suitable patches and hence be exposed to that environment, and low enough not to be overwhelmed by masses of dispersing individuals that are uncoupled to the local environment.

Mass effects indicate situations where the dispersal between patches is high enough to influence not only occurrence but also abundance and population dynamics of organisms. Dispersal rates are therefore higher than what would be required just to colonize local patches, and high in relation to local demographic rates such as births and deaths. Typical examples are source sink dynamics where populations in poor habitats are subsidized numerically by immigration from nearby patches. Mass effects could potentially occur also by pure differences in size between patches, as a significantly larger habitat might satiate the nearby surroundings with emigrants.

Neutral models mean that the fitness of different species is similar and they do not differ in competitive ability or resource requirements. Diversity and abundance is here the result of a balance between ecological drift and speciation (Hubbell, 2001). This is often used as a null model in ecology but it nevertheless predicts some common patterns and is sometimes difficult to reject (McGill, 2003; Volkov et al., 2003). In neutral models, environmental heterogeneity has to be lower than the species specific sensitivity to that heterogeneity, meaning that there still may be measurable environmental heterogeneity but this is not large enough to influence the species. Alternatively, species with high environmental specificity may still display neutral patterns in homogeneous environments.

Thinking of metacommunities in these four conceptual boxes has advantages and disadvantages. The four concepts do not necessarily preclude each other and some metacommunities can be described as a mix of several of them, simply because species are different. Some species might be highly affected by mass effects in one ecosystem, while species sorting is the dominating force for another. There might also be metacommunities that do not seem to fit easily in any of these boxes. The conclusion is that these concepts should be used to the extent that they are useful, to enlighten important processes and improve the understanding of the system in question. They should not be overused and reduce metacommunity theory to merely an exercise in labeling and definitions.

3 Aims of the thesis

The overall aim of this thesis was to investigate different factors that determine the abundance and diversity of animals in spatially structured landscapes. In a few cases, this is a straightforward process of falsifying specific hypotheses. Mostly, however, it amounts to gaging the strength by which different forces and processes determine the distribution and composition of communities. It is a matter of how much, rather than if. This thesis compares the influence of dispersal, habitat size, disturbance, environmental quality, species interactions, and biodiversity in spatially structured landscapes. More specifically, the aims can be broken down according to the four articles:

I Dispersal is a key process in any spatially structured community. Effects of habitat fragmentation, indicating differences in dispersal rates between landscapes of differing connectivity was already demonstrated using the same model system as in this thesis (Gilbert et al., 1998; Gonzalez et al., 1998; Gonzalez and Chaneton, 2002; Hoyle, 2005). However, the range of dispersal rates for different organisms and the time needed to recolonize empty patches was not well known. In addition, the influence of patch size on overall dispersal was not well established, nor were the effects of the methods of defaunating local habitat patches on habitat quality. The aims of paper I were therefore to quantify effects of within habitat, mainland to island and island to island dispersal, using defaunated patches as the target habitats. The experiment in article I manipulated fragmentation and isolation distance from a main dispersal source, as well as size of dispersal sources.

II The ability of habitat corridors to provide rescue effects has received mixed support in earlier studies (Gilbert et al., 1998; Hoyle and Gilbert, 2004; Hoyle and Harborne, 2005; Staddon et al., 2010). We hypothesized that rescue effects would be most profound when the difference in dispersal rates in habitat corridors and surrounding matrix was high, as well as when the environmental conditions were poor, leading to small and fluctuating populations. The experiment in article II examined these hypotheses by manipulating connectivity through habitat corridors, as well as matrix quality and environmental quality in fragmented replicate landscapes.

III Earlier studies have found support for community relaxation (community disassembly) as a result of habitat fragmentation (Gonzalez, 2000; Gonzalez and Chaneton, 2002). Another key process that may be affected by the spatial structure of landscapes is community assembly. Together, these processes govern how communities react to and are reconstituted after e.g. fragmentation and disturbance events, qualities that sometimes are referred to as the resilience of a community. Article III investigated the effect of connectivity and biodiversity on these processes by manipulating connectivity and diversity in replicate landscapes (Figure 4).

IV Studies using this model system have so far spanned relatively short time periods, where transient dynamics may play a dominant role. Although this does not disqualify them, findings of lasting effects would increase their generality and relevance to other systems. In addition, the relative influence of environmental explanatory factors and spatial factors was not well known. Article IV is a study of abundance, species richness, and community composition of mature communities in naturally occurring patches of varying connectivity, isolation, and environmental conditions.

4 Methods

4.1 Working with model systems

A few words could be said about model systems in general. The defining feature of a model system is that the findings are applied to other systems. The alternative is when the findings are foremost applied in the same system. It follows, therefore, that the value of an experiment with a model system hinges on the generality of the results. It should also be noted that there are more model systems in ecology than one might first think. Any system could be said to be a model system in this regard, if its results are applied to other systems. If we review the current ecological literature, we

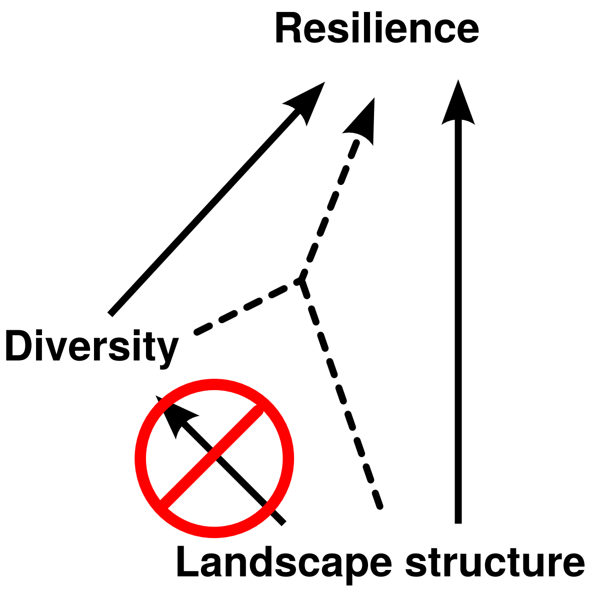


Figure 4: Article III studied how landscape structure, diversity and their potential interactions influenced resilience, interpreted in terms of how the community withstands changes in landscape structure and how well the community is reconstructed after severe disturbance events. Resilience was therefore addressed through the processes communty disassembly and community assembly. Direct influence of landscape structure on diversity was an expected confounding factor, and was controlled for by individually manipulating landscape structure and diversity.

will find that a large portion of the studies try to generalize at least parts of their results. The generality and applicability of each model system is evaluated case by case, depending on what inference the author is trying to make. It is then a misunderstanding to disqualify the applicability of results from model systems, simply on the grounds that they come from model systems.

4.2 Types of answers

Some scientific fields try to formulate general laws about how the world works, and this is sometimes seen as the obvious goal of science as a whole (Nagel, 1961). The process of revealing these laws is stereotypically described as a series of deductive steps, where hypotheses are progressively falsified (Popper, 1959; Platt, 1964). However, this is a simplified and often misrepresentative description of how the natural sciences work, particularly in ecology. The existence of natural laws in ecology is a matter of debate (Lawton, 1999; Colyvan and Ginzburg, 2003; Lange, 2005), as well as the existence of natural laws altogether (see e.g. Van Fraassen, 1989). The trade off between being general but vague, or specific but limited, is ever present in ecology. If ecological laws exist, they are not the bread and butter of ecology, at least not as it is practiced today. Clear falsifications of hypotheses are arguably not the typical way by which ecology moves forward. More suitable is a description where a multitude of hypotheses are simultaneously entertained with varying degrees of evidence and applicability (Chamberlain, 1890). These hypotheses or models may capture different aspects of a phenomenon or a system, and their use may depend on the aim of the researcher.

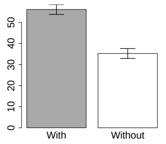
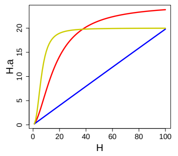
1. Proof of concept - does it exist? • Can we find effects of fragmentation on biodiversity? - yes/no • Can we manipulate landscape structure so that it affects resilience? - yes/no	
2. Description of pattern - how does it look? • Response curves, correlations • e.g. heterogeneity ~ biodiversity	
3. Description of process - how does it work? • What is the mechanism? • e.g. when and why does fragmentation and connectivity matter?	$\frac{dP}{dt} = rP\left(1 - \frac{P}{K}\right)$

Table 1: Schematic diagram of the different levels of explanation in ecology. The applicability of the results and potential for generalizations are judged mainly on a case by case basis. This judgement gets easier the closer we get to fully understanding the processes.

Still, ecology moves forward. We now know more about how the natural world is constructed and how species interact with each other and the environment than before. Step by step, experiences from different ecosystems accumulate which allow us to better judge what the important processes are in various locations. In addition, our methods for incorporating these findings in mathematical models increase, which improves our ability to predict future events (Hilborn and Mangel, 1997). But the models seem to, by necessity, have to sacrifice either realism, generality or precision (Levins, 1966).

Results from ecological studies comes at different levels, from proofs of concept, through discovery of patterns, to description of processes (Table 1). Our ability to judge the applicability and generality of the findings increases with the increased detail of our understanding of the phenomena. If we fully understand an ecological process, we should be able to judge whether it is applicable to a new system or not. Generalizations of processes should not be hindered by differences in species identity, environment or spatial scale, since a full understanding of the process would enable us to evaluate the relevance of those differences.

From this discussion, it seems that model systems are commonplace in ecology, although they may not be all that apparent whenever they operate on the same scale as the "target system". Their applicability is evaluated each time an inference from one system to another is made. This evaluation is aided by increased detail in the understanding of the process in question. The chances of getting usable results increases if the experiments are simple. Since a PhD-project is relatively short, a trade off has to be made between the detail of the results and efficiency of the experiments, and most results of this thesis are of the proof of concept type. However, several patterns are also described, as well as some processes.

4.3 The bryophyte-microarthropod model system

The model system used here is the bryophyte-microarthropod system (Gonzalez et al., 1998; Srivastava et al., 2004). This model system has been used successfully to investigate effects of spatial structure and disturbance on maintenance and recolonization of microarthropod communities (e.g. Gilbert et al., 1998; Starzomski and Srivastava, 2007; Staddon et al., 2010), as well as species area relationships (Hoyle, 2004). Moss patches offer a convenient way to manipulate the spatial structure of landscapes in a controlled manner and achieve a high level of replication. The moss contains a rich fauna of detritivores, fungivores, and predators. The most species rich group is oribatid mites, which are relatively slow dispersing detritivores and fun-

(a) Locality "B" used in experiment III.

(b) Experimental setup of experiment II

Figure 5: Source material and an example of a finished set up of the bryophyte-microarthropod model system.

givores. Many species are parthenogenetic (can reproduce asexually) and manage one to several generations a year, depending on environmental conditions. Juvenile oribatids are especially vulnerable as prey for predatory mites as these have not yet developed a hard exoskeleton. Predatory mites belong to the order and suborder Mesostigmata and Prostigmata, but are in these experiments dominated by Prostigmata. Collembola is the final taxonomic group studied in this thesis. They are relatively fast dispersing detritivores that also constitute prey for predatory mites and seem also to be more sensitive to environmental stress than oribatid mites. The size of the animals range from approximately 0.5 mm to 4 mm, collembolans having the largest representatives.

Sampling of the moss patches is by necessity destructive. The moss cushions are placed in a "Tullgren funnel" which is a metal funnel suspended upside down with a light bulb over it. The sample is laid on top of the funnel, beneath the lamp, on a metal mesh. The lamp creates a light and heat gradient through the sample, which makes the animals move downwards and finally fall through the funnel into a container filled with 70% ethyl alcohol.

4.4 Data and statistics

Working with microarthropods has some definite advantages. They move sufficiently fast to measure dispersal within a PhD-project, and sufficiently slow to make the spatial scale of their landscapes manageable. They are also abundant, and collecting vast amounts of animals is easy. Identifying the collected specimens is not as easy. Because of their size, densities, and sometimes cryptic taxonomy, it can be a challenge to properly identify them. Combining the experiments in this thesis, we have collected over 800 000 animals. For practical reasons, I have not been able to identify the organisms to species level. The exception is article IV where the identification was done by Niklas Lindberg. In article I, Oribatida species was identified as morphospecies as this experiment had relatively small abundances. These groups conformed relatively closely to true unique species. In the rest of the articles, oribatid mites have been identified to family or genus level which in the articles is referred to as morphospecies, even though the morphospecies generally consisted of several true species.

Soil animals have the capacity to reproduce fast under the right conditions and are often patchily distributed. One sample may contain 10 Collembola and another sample only 1 meter away may contain 3 000. Samples of soil animals therefore often show large variation, and it is sometimes necessary with large sample sizes to capture trends in the data. Experiment 1 consisted of 64 measured island habitats and 46 measured mainland habitats. In retrospect, it would have been beneficial with even more island habitat samples as we saw some indications of patterns that were not statistically distinguishable. Experiment II consisted initially of 96 replicate landscapes of in total 384 habitat patches. Close before the sampling date, magpies interfered and destroyed a large portion of the samples, so that the end sample size was 62 landscapes and 239 patches. Despite a bias in the data set, we were able to analyze all treatments using mixed modeling techniques. In retrospect, the avian intervention was perhaps a blessing in disguise since the remaining samples contained over 500 000 individuals. Experiment III consisted of 36 landscapes with in total 216 sampled patches. There were no obvious indications of undersampling in that data. The natural experiment in article IV would probably have benefited from more extensive sampling since it contained in total 54 samples, but here a constraint was the amount of patches of comparable qualities.

Measurements of counts of individuals were modeled as a Poisson variable, since the number of times an individual occurs within an area is typically Poisson distributed. However, the variance of the Poisson distribution is by definition equal to the mean, while count data often has a larger variance than the mean. This is called overdispersion and has to be accounted for in order to make the proper inferences. In article I, this was compensated for by using penalized least squares and a quasiPoisson distribution. In articles II, III and IV, overdispersion was modeled by including an individual random effect for each sample, creating a lognormal-Poisson mixture distribution (Hinde, 1982).

The most common statistical tool in this thesis was generalized mixed models, where the logarithmic mean of each sample was described by a linear additive model. Replicate landscape identity was included as a random effect, preventing pseudo-replication. Since the parameter estimates of the additive explanatory factors were estimated through the log link, these estimates were generally exponentiated (back-transformed) and interpreted multiplicatively, resulting in statements such as "abundance was 20% lower in fragmented habitats than in continuous habitat".

In article II, measurements of diversity was partitioned into α,β, and γ parts multiplicatively, i.e. $\gamma = \alpha * \beta$ (Jost, 2007, 2010). Statistical significance of these components was determined by randomization tests where sample identities were randomized to create a null distribution against which the actual measured diversity components were compared.

In article III, randomization tests were again used to determine to what extent community assembly and disassembly deviated from what would be expected by random colonization and extinctions of individuals, respectively.

Rather than following an automated or fixed criteria model simplification routine, model averaging from the multimodel inference framework was used in articles II-IV (Burnham and Anderson, 2002; Whittingham et al., 2006). This has the advantage of not disregarding models of similar explanatory power due to arbitrary cut off values. In these analyses, averaged estimates were reported, based on model averaging of the candidate models constituting the top 90% of cumulative weights.

5 Results

The results of this thesis can be summarized in three sections. First, fragmentation has important effects on communities. These effects depend on species characteristics and can therefore change community composition. Second, factors such as spatial structure and aspects of environmental quality can interact with each other, creating sometimes counterintuitive end results. Thirdly, even though communities are influenced by factors that are relatively consistent, population dynamics still play an important role.

I discuss these aspects in turn.

5.1 Effects of fragmentation

Many of the more intricate results of this thesis are specifications, conditions, or divergences from the blanket statement that fragmentation is bad. Still, the negative effects of fragmentation that were found should not be understated. Habitat fragmentation is a global current problem and the results of this study indicates major negative effects of fragmentation. In both articles I and IV, I recorded large differences of abundance and also differences in species richness between habitat patches located within a large mainland, and isolated, smaller habitat patches. Article I measured the recolonization of defaunated patches. Habitat patches that were surrounded by populated habitat showed markedly higher abundances of Oribatida mites than fragmented patches (means = 65.5 vs. 8.4. t-test, P=0.012, Figure 6). Article III also show clear signs of non-random species loss as a result of habitat fragmentation.

Article IV measured the lasting effects of spatial and environmental determining factors on abundance, richness, and community composition. Also here, the differences between mainland habitats and fragmented islands were large. Abundances were approximately 2 to 6 times higher in mainland patches than in fragmented patches of equal size, depending on taxonomic group. Species richness was approximately twice as high in mainland patches than in fragmented patches of similar size.

5.2 Interactions of landscape qualities

One of the main results from this thesis is that the effects of spatial structure is context specific. In other words, the effect of spatial structure is subject to several types of interactions, and some of these interactions can lead to counterintuitive results. One part of this specificity is that species and higher taxonomic groups react differently to landscape structure. Species differ in their dispersal capacity and rate, which naturally influences their response to fragmentation. An example of this is the vast difference in abundance of oribatid mites and collembolans in the fragmented patches in article I. Already at an isolation distance of 5 cm from the mainland, oribatid mites were significantly reduced while collembolans did not show any declines. In fact, the highest densities of collembolans were recorded in patches 3 meters from the mainland, suggesting that some collembolans might even benefit from habitat fragmentation.

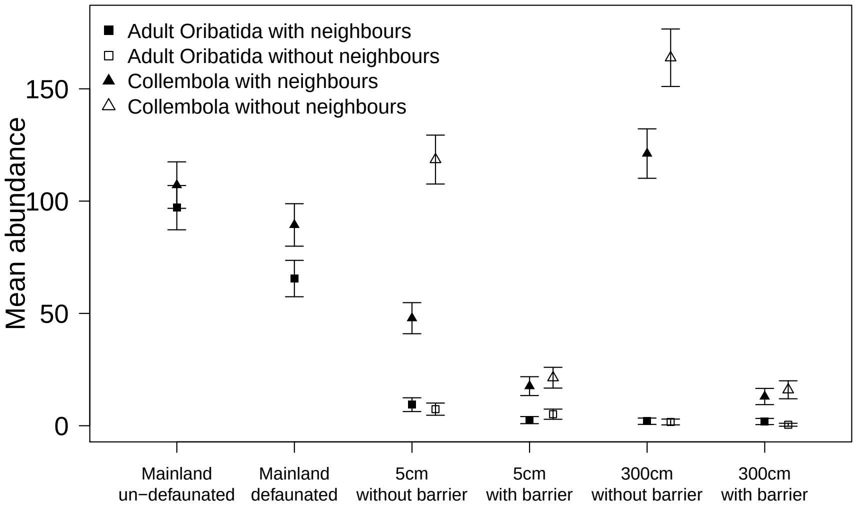


Figure 6: Mean abundances of adult Oribatida mites and Collembola in experiment I. Error bars are square root of means.

Another part of the context specificity of spatial structure is that different landscape qualities may interact. Article II shows strong interactions between habitat corridors and matrix quality. Although this was hypothesized, the interaction was in the opposite direction than expected. We hypothesized that the beneficial effect of habitat corridors would be the greatest when the difference between dispersal rates in corridors and surrounding matrix was the largest. In contrast, the collembolans and predatory mites strongly decreased in landscapes with corridors, when the corridors were surrounded by a harsh matrix. Oribatid mites were unaffected by this interaction. In landscapes with poor matrix, presence of corridors decreased abundance of collembolans (39% reduction) and predators (46% reduction), whereas this negative effect of corridors was not visible in landscapes with good matrix. In good matrix landscapes, corridors actually had a tendency to increase predator abundance (18% increase). This result indicates that habitat corridors acted as sinks for collembolans and predatory mites in landscapes with harsh surrounding matrix. The likely mechanism was susceptibility to edge effects such as drought, and increased chances of non-optimal dispersal into the matrix. As the matrix consisted of coarse gravel, most individuals that ventured this route were probably lost from the system permanently. The more tentative, slower dispersal mode of oribatids, relative to the faster and more erratic collembolans (sometimes springing with their forcula) may explain the large differences between the two groups.

A third example of context specificity is that spatial structure may influence species interactions. Article II show signs that fragmentation can create a predatory release, which prey species may benefit from. The measurements of potential prey groups collectively showed a trend of increase in fragmented landscapes, while this was not the case for predatory mites. In addition, habitat corridors increased the abundance of predatory mites (at least in landscapes with good matrix) but decreased the abudundance of the prey group oribatid mites. The decrease in abundance of oribatid mites was not likely due to corridors themselves having negative consequences for oribatids, as there were no interactions between corridors and matrix quality, as with predatory mites and collembolans. Predators have been found to be especially sensitive to habitat fragmentation also in earlier studies (Gonzalez and Chaneton, 2002; Hoyle, 2005). Recently, Staddon et al. (2010) explained decreased oribatid abundances with increased predation pressure in landscapes with corridors in a similar experimental setup.

5.3 Dynamics

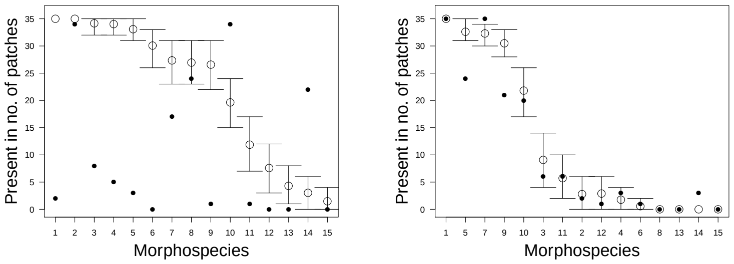
So far, I have discussed influences of potentially static qualities of spatial configuration, species identity, and environmental quality; factors that have a lasting influence on this metacommunity (article IV). However, the results of this thesis also point to the importance of processes and dynamics on shorter time scales. Experiments that were sampled during extended time periods showed large seasonal variability in abundance. Most species displayed a burst of activity in spring and autumn and showed relative inactivity in the dryer summer periods. Small habitat patches do not retain moisture as well as larger patches and suffer from repeated desiccation during dry periods, even though small patches can be partially re-wetted by dew, even during summer nights. When winter comes and temperatures drop below zero, activity is suspended until the thawing in spring.

Several findings in this thesis together suggest that a large mainland can influence even distant patches significantly, and that the influence comes in the form of seasonal bursts of emigrants. In article I, I placed defaunated habitat patches at varying distances from a large mainland. Even at 3 meters from the mainland, which is an uncommonly large distance from surrounding mainlands, the influence of the mainland was large. Collembolans had recolonized the defaunated patches to abundances comparable to those in the mainland, and their abundance was actually lowered by nearby neighbor patches. Oribatid mites received about as many dispersers from the three nearby neighbor patches as from the mainland 3 meters away. Considering that the available number of emigrants from smaller neighbor patches was limited, and emigrants from the large mainland come in practically unlimited supply, the influence of the mainland will likely accumulate over time.

The overall negative effects of fragmentation—where seasonal desiccation may be the main proximate cause of local extinctions—coupled with a large number of colonizers from the mainland, paints a picture of seasonal dynamics in the naturally fragmented habitat islands. Local fragmented patches close to mainlands are probably either in a state of community assembly or community disassembly, depending on the season.

Resilience is a much sought after quality of ecosystems, not least in anthropogenically altered landscapes where habitat fragmentation is common. The term is, despite several strict definitions, multifacetted (Brand and Jax, 2007). When we speak of resilience, we could mean either the time required for a population or a community to return to a starting condition after a disturbance, or the range of conditions under which a system will return to an equilibrium, or even - and perhaps most common in applied cases - the ability of a system to provide certain functions or services when under the influence of an extraneous stressor. The processes that underpin the qualities we are after however, is often community disassembly or community assembly; how communities lose or retain species in the face of some disturbance, or how communities are reconstituted after a disturbance. Resilience, as influenced by diversity and landscape structure (Figure 4), was therefore investigated with this in mind.

Community assembly in fragmented habitats was shown to follow random colonizations of individuals from the surrounding species pool relatively closely (article III). In contrast, community disassembly following a fragmentation event was distinctly non-random. Species clearly reacted differently to habitat fragmentation. Figure 7 shows that disassembly did not occur as would be expected from a random loss of individuals, whereas community assembly was clearly related to the regional abundance of different morphospecies. The two processes clearly operated in different ways. The evaluation of that system's resilience was therefore dependent on whether we target community assembly or disassembly. Moreover, the answer also differed as to whether we measured these processes on an absolute or relative scale, since the more diverse communities lost a disproportionate amount



(a) Community disassembly. *(b)* Community assembly.

Figure 7: Community disassembly and assembly in fragmented landscapes. Empty circles represent expected occurrence if community disassembly and assembly followed a random loss of individuals, and random gain of individuals, respectively. Black dots represent observed occurrence. For disassembly (7a), species rank is based on initial rank abundance at the start of the experiment. For assembly (7b), species rank is based on the rank abundance of the surrounding pool of individuals at the end of the experiment. Morphospecies numbers are the same in both graphs. Error bars represent 95% confidence intervals from 1000 randomizations.

of species as a result of fragmentation, but still retained more species after fragmention, than less diverse communities.

Habitat fragmentation is sometimes discussed in terms of extinction thresholds, indicating the amount of habitat that can be lost before the amount of habitat becomes too small, and species are regionally lost (Bascompte and Solé, 1996). Although estimates of a single value of such a threshold have been sought both empirically (Andrén, 1994), as well as analytically (Hanski and Ovaskainen, 2000, 2002), it is recognized that species react differently to habitat fragmentation and may display different extinction thresholds (Pardini et al., 2010). It is possible that the communities in article III disassembled differently than according to a random loss of individuals—as a consequence of the species having different extinction thresholds—and that the communities reassembled essentially according to random colonization of individuals, since the remaining landscape is fragmented above the remaining species' extinction thresholds.

6 Conclusions

6.1 Synthesis and emergent answers

Figure 2 lists possible influencing factors on community composition. This thesis contains evidence of all six different kinds of influences. The results are of varying levels of explanation (Table 1), from proofs of concept to at least the beginnings of an understanding of the processes.

Fragmentation had a major influence on abundance, diversity, and community composition in the four studies in this thesis. Decreasd habitat size, loss of connectivity, and increased isolation distance generally decreased microarthropod abundances and diversity. We saw no effect, however, of connectivity as long as the patches were at least minimally connected (article III). Species characteristics and interactions also combined with fragmentation, creating winners and losers in fragmented landscapes. Highly dispersive species (e.g. Collembola) coped with fragmentation relatively well, but could be negatively affected by linear elements exposing them to harsh matrix conditions.

Environmental quality clearly affected abundance and diversity, and there were responses that were specific to species or groups of species, giving rise to changes in community composition. For instance, Collembola and predatory mites were more strongly affected by the environmental stress treatment (mainly drought) than oribatid mites in article II. Composition of non-oribatid mites was also shown to be continuously affected by environmental factors under natural conditions; environmental factors that likely affected moisture content (article IV).

Although the communities overall responded to manipulations and natural variation of determining factors, there was considerable unexplained variation. Habitat patches with practically unmeasurable differences in environmental quality still differed in composition and population trajectories. It thus seems to be significant randomness in this system. However, overall, the species specific responses to differences in spatial structure and environmental quality generally speak against the applicability of neutral models.

We saw several signs of species interactions through predation (articles II and III), but less clear evidence for competition. Collembolans could potentially outcompete oribatids in highly fragmented and disturbed landscapes due to their high capacity for dispersal, but the experiments did not last long enough to explicitly test this, and the results in article IV showed no signs of this. Oribatid species reacted to fragmentation differently, suggesting competitive differences between species (article III). Still, the remaining species pool did not show any signs of competition in the colonization of empty patches.

Disturbance significantly altered patterns of abundance and diversity (articles I, II, and III). Strong seasonal variations, large differences in size of source patches and large differences in local population numbers due to local population dynamics suggest that this system is better characterized as a system in change than in equilibrium.

The model system was investigated under natural conditions or close to natural conditions in article IV and I, respectively. In both studies, there was a large nearby mainland that had a dominating influence on the fragmented patches. Although the isolation distances were large enough to represent substantial dispersal barriers for many species, the probability of colonization from the mainland is probably so high that the system is best described as a mainland-island system at those sites and not a metapopulation in the strict sense (cf. Harrison et al., 1995).

Variance partitioning (article IV) revealed a dominating influence of spatial variables on community composition, as opposed to environmental variables. Only non-oribatid mites showed a substantial influence from environmental factors. This strenghtens the case of manipulative experiments that treat possible environmental factors mostly as nuisance parameters. Of the spatial variables, habitat size generally had more explanatory power than isolation distance. If one were to rank the measured components of fragmentation in order of importance, based on the studies in this paper, it would probably be 1) habitat area followed by 2) connectivity to significant dispersal sources and lastly 3) isolation distance.

6.2 Some take home points and implications

There is a danger in simplification. I will therefore not attempt to summarize this work further. What follows is rather a collection of things that one should be observant of when working with habitat fragmentation, either at a desk in a nature conservation agency, or with a chainsaw in your hands. So in the spirit of primary school (and my old teachers will be dismayed by my lack of development), I end with a list of bullet points (Visste du att: ...?).

- Habitat fragmentation has important consequences for ecological communities. It is likely to result in declines in abundances and species loss, both locally, and in case of severe fragmentation, regionally. This species loss can be difficult to predict as the response often is species specific, and sometimes some species or groups of species may actually benefit from fragmentation.

- Influence of spatial characteristics is context dependent. An example of this is that mitigating measures, such as the construction of habitat corridors, may have unexpected consequences due to interactions between spatial structure, environmental conditions, and species interactions.

- When thinking of fragmentation, consider the total amount of dispersing individuals, not just isolation distance. Habitat size, or dispersal from a large mainland, may dominate over more intellectually attractive qualities such as connectivity and isolation distance.

- Some good dispersers may require things that are lost in fragmented systems. Throughout the experiments in this thesis, predatory mites were especially susceptible to habitat fragmentation, despite their supposed dispersal ability matching or succeeding that of their prey. Overall, dispersal capacity was a poor indicator of the species sensitivity to habitat fragmentation, indicated by the low % of explanation by isolation distance in article IV and the sometimes unintuitive responses to fragmentation in articles II and III.

- When talking about the resilience of a community, it may be beneficial to focus on the processes behind the patterns, community disassembly and assembly, on either a relative or an absolute scale. Ask the questions: "What process are we interested in?" and "How can we influence it and predict it?"

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Populärvetenskaplig sammanfattning på svenska

Mänsklighetens största påverkan på jordklotet har hittills varit förändringen och förstörelsen av naturliga livsmiljöer, eller habitat. Som exempel kan nämnas att ca 70% av de temperade skogarna har konverterats, främst till jordbruksmark, och att arter idag dör ut mellan 100 och 1000 gånger fortare än vanligt till följd av mänsklig påverkan. Vissa menar till och med att vi bör benämna den nuvarande tideräkningen som Antropocen, vilket betyder att mänskligheten numera är den mest betydande kraften som omskapar planetens topografi och klimat. Det finns heller inga tecken på att den här utvecklingen kommer att avta, snarare fortsätter det totala resursutnyttjandet att öka exponentiellt. Kvar av de ursprungliga habitaten blir allt mindre brottstycken, med andra ord fragmenteras habitaten. Denna utveckling utgör det vetenskapliga grundproblemet som ligger bakom denna avhandling. Vi vet nämligen inte vad utvecklingen med utökad habitatfragmentering kommer att få för konsekvenser. De mest grundläggande konsekvenserna känner vi till, att arter och därmed de funktioner som arterna utför försvinner i takt med förstörelsen av deras habitat. Men vi vet inte detaljerna; vilka och hur många arter som försvinner, och hur vi ska förvalta de habitatfragment som finns kvar för att bäst behålla arter och funktioner.

När man delar upp habitat i isolerade beståndsdelar kan man välja tre sätt att se på det bildade landskapet. Det första är att ignorera uppdelningen och se den totala mängden kvarvarande habitat som en enhet. Det är en möjlig väg om arterna som lever i dessa fragment sprider sig emellan de olika fragmenten i stor uträckning, så att isoleringen inte spelar någon roll. Det andra sättet är att se de olika fragmenten som helt isolerade. Då kan vi undersöka och förstå ekosystemen i varje fragment separat, ett tillvägagångssätt som fungerar om det inte förekommer någon spridning alls av organismer mellan habitatfragmenten. Bägge dessa sätt beskriver alltså i praktiken ett enda habitat i taget. Det här var också det klassiska sättet att förhålla sig till ekosystem innan effekterna av habitatfragmentering blev för uppenbara för att bortse ifrån, och innan synen på de ekologiska systemen förändrade sig ifrån att huvudsakligen uppfattas som statiska, till att mer och mer poängtera de dynamiska, föränderliga egenskaperna som har skapat och fortsätter skapa våra växt- och djursamhällen. Numera vet vi att habitatförstörelse och fragmentering har allvarliga konsekvenser för ekosystemen. Vi vet också att när habitat delas upp i brottstycken får spridningen av organismer mellan de kvarvarande habitaten potentiellt stor betydelse.

Populationer som sammanlänkas genom spridning av individer kan ses utgöra en större enhet, en så kallad meta-population. Även om lokala populationer då och då dör ut, finns en potential för återkolonisering från andra, fortfarande livskraftiga populationer. Det är överlevnaden av metapopulationen som helhet som har den avgörande betydelsen och naturområden börjar därför alltmer beskrivas på landskapsnivå, dvs att man tar hänsyn till hur den långsiktiga överlevnaden av arter påverkas av hela landskapets innehåll och struktur. På samma sätt kan man prata om att samhällen av olika arter, dvs alla de arter som lever tillsammans på ett och samma ställe, också är sammanlänkade med varandra genom spridning av individer sinsemellan. Det är vad som menas med ett meta-samhälle, eller metacommunity som återfinns i titeln på avhandlingen.

Teoribygget kring meta-samhällen har ambitiösa mål men är fortfarande i sin barndom. Det övergripande målet är att kunna förklara vad som avgör hur organismsamhällen av olika slag bildas och består. Huvudsakliga beståndsdelar i den förklaringen är 1) lokala miljöförutsättningar och hur olika arter påverkas av dessa, 2) samspel mellan arter inom varje lokalt samhälle, 3) spridning av individer mellan samhällen och 4) lokala och regionala störningar av miljön. Exempel på praktiska frågor i dessa områden är 1) “Hur påverkas markvegetationen i två olika täta skogsdungar av skillnaderna i ljusinsläpp?”, 2) “Kommer en ökad rovdjursstam minska betestrycket på unga trädplantor?”, 3) “Hur påverkas pollinerande insekter av det ökande avståndet mellan skogspartier” och 4) “Vilken effekt får en tät avverkningsfrekvens på långsamt växande arter?”. Alla dom här aspekterna är potentiellt viktiga för arter som lever i fragmenterade miljöer, och uppskattningen av deras relativa betydelse är en huvuduppgift för meta-samhällsteori. I vissa samhällen kommer spridning mellan olika habitat helt avgöra hur de lokala samhällena ser ut. I andra kommer skillnaden i miljöförutsättningar mellan habitat vara helt avgörande osv. Relevansen av alla dessa faktorer skiljer sig från fall till fall, och är av avgörande betydelse för hur vi bäst ska förvalta rumsligt strukturerade miljöer. Det är med detta som bakgrund denna avhandling har kommit till.

En försvårande omständighet för experiment på det här området är att manipuleringar på landskapsnivå ofta är svåra eller omöjliga att genomföra. Jag har försökt kringå det problemet genom att minska skalan, både på livsmiljöerna och på organismerna. Jag använder mig av ett modellsystem som består av sjok av mossa, och de små ryggradslösa djur som lever däri. Kanske i motsats till vad man förväntar sig innehåller dessa miljöer rika samhällen med flera trofiska nivåer, dvs både nedbrytare, växtätare och rovdjur. Organismerna jag har studerat är främst pansarkvalster och hoppstjärtar. Genom att sätta samman mossa har jag byggt upp miniatyrlandskap där hundratusentals djur har ätit, ätits, spridit sig, fortplantat sig och dött ut. Allt med tanken att resultaten i överförd bemärkelse kan säga något om de landskap som omger oss själva och som vi också påverkar.

Genom tre experimentella försök och en inventering av naturliga landskap har jag undersökt hur samhällen faller ihop och byggs upp, beroende på fragmenteringsgrad, storlek, avstånd till spridningskällor, artsamspel och miljökvalitet hos enskilda fläckar av habitat.

Resultaten visar på tydliga effekter av habitatfragmentering, men effekterna var inte negativa för alla arter. Olika arter interagerade vilket gav upphov till oväntade effekter av fragmentering. Predatorer visade sig överlag vara extra känsliga för fragmentering vilket i några fall ledde till att antalet av deras bytesdjur ökade i fragmenterade miljöer. Olika landskapselement visade sig också samverka med varandra och skapa oförsägbara och icke intuitiva resultat. Till exempel så kopplade jag samman separata habitat med spridningskorridorer. Det här är en populär naturvårdsåtgärd för att sammanlänka isolerade habitat med syfte att öka den effektiva storleken på livsmiljöer, och förhindra lokala utdöenden genom att rädda temporärt svaga populationer med inspridning av nya individer. Tanken är att spridningskorridorer ska vara speciellt viktiga där de miljöer som omsluter habitaten är av dålig kvalitet eller är svåra att korsa, till exempel högintensiva jordbruk eller motorvägar. I mitt försök ledde bildandet av spridningskorridorer visserligen till ökad spridning emellan habitatfragmenten, men i de landskap där omgivningen var av speciellt dålig kvalitet ledde spridningskorridorer ändå till minskade populationer av djurgrupper som är relativt goda spridare. Spridningskorridorerna ledde helt enkelt till att individer spreds ut i dåliga miljöer där de gick under, istället för att stanna kvar i fläckarna av livsdugligt habitat. Dessa två effekter visar på faran av att schablonmässigt föreskriva spridningskorridorer utan att ta hänsyn till samspel mellan arter och mellan landskapselement.

Ett annat resultat är att djursamhällen bröts samman på ett oförutsägbart sätt till följd av habitatfragmentering. Förlusten av arter följde inte vad som kunde förväntas av ett slumpässigt bortfall av individer. Med andra ord, känsligheten för habitatfragmentering skiljde sig markant åt mellan olika arter. Tvärtom följde uppbyggnaden av djursamhällen förutsägbara mönster i habitat som genomgått en kraftig störning. Återkoloniseringen av störda habitat var alltså en återspegling av den omgivande förekomsten av individer. Både motståndskraft mot störning och habitatförstörelse samt förmåga att återbildas efter störning är centrala kvaliteter hos fragmenterade miljöer, som ibland brukar samlas inom begreppet resiliens. Mina resultat visar dock att dessa processer fungerar på distinkt olika sätt. En framgångsrik naturvård borde därför uppmärksamma vilken av dessa processer som är den viktiga i varje specifik situation.

Ett ytterligare resultat är att fragmenterade, mindre habitat som befann sig i närheten av ett större habitat, likt skärgårdsöar utanför ett fastland, var starkt påverkade av inspridning från fastlandet. Mängden individer som spred sig från det större habitatet var helt enkelt så stor, att även för organismerna betydande avstånd överbryggades. "Skärgårdsöarna" var i dessa fall alltså starkt påverkade av förekomsten av livskraftiga populationer i fastlandet. Konsekvensen är att kontinuerligt stora populationer på fastlandet förmodligen spelade en större roll för den långsiktiga överlevnaden av bestånden på öarna än storleken hos de lokala bestånden på öarna vid ett givet tillfälle.

Slutgiltigen hade variationen av rumsliga kvaliteter; habitatstorlek, habitatsplittring och avstånd till spridningskällor; större påverkan på de undersökta djursamhällena än skillnaden i miljökvalitet mellan enskilda habitat. Sammantaget visar resultaten på vikten av att förvalta naturen på landskapsnivå och att uppmärksamma de betydande effekter som spridning av individer kan ha på både lokal och regional överlevnad i fragmenterade miljöer.

Tack

En insikt som gång på gång har gjort sig påmind under de här åren är att inget går av sig själv. Varje förberedelse, beslut, misstag, lärdom och punkt (.) måste genomföras. Och det faller naturligtvis på doktorandens lott att genomföra det. Därför är det ändå förvånande att tiden har gått så pass fort. De här fem åren har tagit mig från ett fabriksgolv med snäva utsikter till, tja, någon annanstans i alla fall, men med mycket bättre framtidsutsikter.

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Punkt.