Diss. ETH No. 17810

# Density regulation:

# Linking theory and applications to understand population- to community-level dynamics and responses to environmental change

A dissertation submitted to
ETH ZURICH

for the degree of
Doctor of Sciences

presented by
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2008

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# Summary

Intra- and interspecific density regulation, as it results from competitive interactions between con- and heterospecifics, affects population and community dynamics and thus can interfere with both single species survival and multi-species coexistence. This thesis aims at a better understanding of how density regulation operates and how it modifies the impacts of habitat fragmentation and climate change on species and community persistence. The approach builds upon mechanistic simulation models of single species and communities of species and is twofold: First, hypothetical species are investigated to analyse basic principles and to derive general hypotheses; second, real species are investigated to test model applicability and to derive specific conclusions.

Results from a generic, single-species model demonstrate that species, differing in the mechanisms of density regulation, require different landscape characteristics: Compensating species benefit from strong patch connectivity, whereas over-compensators are prone to spatially synchronised extinctions and thus suffer from too strong connectivity (chapter 1). Adapting the model to experimentally derived Tundra vole dynamics demonstrates that even conditional (density dependent) dispersal is not able to reduce the risk of spatial synchrony through over-compensatory density regulation (chapter 2). Thus, the mechanism of density regulation has to be considered in conservation planning.

Based on the better understanding of the role of density regulation in single species population dynamics I turned to species communities. Analysis of a generic, two-species model reveals over-compensatory density regulation as a potential mechanism of coexistence and demonstrates how this mechanism works (chapter 3). Coexistence is promoted by the over-compensator's tendency to generate fluctuations from which it suffers and the competing species' tendency to dampen these fluctuations from which it benefits. The detection of this new coexistence mechanism allows for a comparison of communities that coexist through over-compensation with those that coexist neutrally. This comparison contributes to the recent and important debate on the relative roles of different coexistence mechanisms in structuring communities. The simulation results show that communities relying on coexistence through over-compensation are more likely to occur in well-connected landscapes with high habitat availability while communities relying on neutral coexistence are more likely to occur in strongly fragmented landscapes. These communities also respond differentially to synergistic

threats of climate change and fragmentation: Communities relying on over-compensation are particularly sensitive to climate change, while neutral communities are much more sensitive to a further increase of fragmentation (chapter 4). Therefore, species' coexistence mechanisms and interspecific interactions should be taken into account when prioritizing conservation actions to mitigate impacts of fragmentation and climate change.

Results from the theoretical studies provided the basis to confront the model with count data of a multi-species small mammal community in forest patches of the Atlantic Brazilian rainforest (chapter 5). The model calibration led to a better understanding of the mechanisms involved in structuring this highly diverse but endangered community and revealed that both neutral and niche-based coexistence dynamics strongly influence community structure. Moreover, the parameterized model predicts an increase in spatial heterogeneity of the community even if assuming present landscape fragmentation patterns to continue in future.

In sum, the results of this thesis contribute to a better understanding of ecological processes emerging from intra- and interspecific competitive interactions, and of how these processes impact spatial population and community dynamics. The thesis reveals the way in which these interactions are responsible for differential responses of both single species and communities to environmental change. With regard to conservation, the results highlight potential drawbacks of common conservation actions and reveal future threats to species and community persistence that may not be apparent yet.

# Zusammenfassung

Inner- und zwischenartliche Dichteregulation entsteht, wenn Individuen einer oder mehrerer Arten miteinander konkurrieren. Dichteregulation beeinflusst Dynamiken in Populationen und Artengemeinschaften und nimmt dadurch Einfluss auf Überleben und Koexistenz von Arten. Ziel dieser Doktorarbeit ist ein funktionales Verständnis von Dichteregulationsprozessen. Das Verständnis dieser Prozesse ist wichtig für eine bessere Abschätzung des Einflusses von Dichteregulation auf die Belastung von Arten und Artengemeinschaften durch Habitatfragmentierung und Klimawandel. Methodisch basiert die Arbeit auf Analysen von mechanistischen Ein- und Mehrartensimulationsmodellen und verfolgt dabei einen zweifachen Ansatz: Zum einen werden Grundprinzipien anhand von hypothetischen Arten untersucht, um daraus generelle Hypothesen abzuleiten; zum anderen wird die Anwendbarkeit der Modelle für reale Arten getestet, und es werden systemspezifische Schlussfolgerungen gezogen.

Ergebnisse des generischen Einartenmodells zeigen, dass Arten auf verschiedene Landschaftsstrukturen angewiesen sind, wenn sie verschiedene Mechanismen der Dichteregulation besitzen: Während kompensierende Arten von starker Konnektivität ihrer Habitatinseln in der Landschaft profitieren, leiden überkompensierende Arten unter zu starker Konnektivität, weil sie besonders anfällig für räumlich autokorrelierte Aussterbeereignisse sind (Kapitel 1). Die Anpassung des Modells an experimentell erhobene Populationsdynamiken der Nordischen Wühlmaus demonstriert, dass sogar (durch die Dichte) bedingtes Dispersal das Risiko von räumlicher Autokorrelation durch überkompensierende Dichteregulation nicht verringern kann (Kapitel 2). Aus diesen Ergebnissen leite ich die Empfehlung ab, Mechanismen der Dichteregulation bei der Erarbeitung von Schutzstrategien zu berücksichtigen.

Basierend auf den Erkenntnissen aus dem Einartenmodell fand eine Erweiterung zu einem Mehrartenmodell statt. Die Auswertung dieses generischen Modells für zwei Arten offenbart, dass überkompensierende Dichteregulation zu Artenkoexistenz führen kann, und zeigt wie dieser Mechanismus funktioniert (Kapitel 3). Während die überkompensierende Art dazu tendiert Dichtefluktuationen auszulösen, aber unter diesen Fluktuationen leidet, dämpft die konkurrierende Art diese Fluktuationen, obwohl sie von ihnen profitiert. Die Entdeckung

dieses neuen Koexistenzmechanismus erlaubt einen Vergleich von Artengemeinschaften, die mittels Überkompensation koexistieren, mit solchen, die aufgrund neutraler Prozesse koexistieren. Dieser Vergleich trägt zu der aktuellen und wichtigen Debatte über den relativen Beitrag verschiedener Koexistenzmechanismen zur Struktur von Artengemeinschaften bei. Die Simulationsergebnisse zeigen, dass Artengemeinschaften, deren Koexistenz auf dem Überkompensationsmechanismus basiert, eher in Landschaften vorkommen, in denen ihre Habitate gut miteinander verbunden sind, während neutral koexistierende Artengemeinschaften häufiger in fragmentierten Landschaften zu erwarten sind. Außerdem reagieren diese Artengemeinschaften unterschiedlich auf synergetische Gefährdungen durch Klimawandel und Fragmentierung: Artengemeinschaften mit Überkompensation sind besonders anfällig für Klimaveränderungen, während Artengemeinschaften mit neutraler Koexistenz deutlich anfälliger auf weiter zunehmende Fragmentierung reagieren (Kapitel 4). Aus diesen Ergebnissen leite ich die Empfehlung ab, dass Koexistenzmechanismen und zwischenartliche Interaktionen berücksichtigt werden sollten, wenn Maßnahmen zur Entschärfung negativer Auswirkungen von Fragmentierung und Klimawandel geplant werden.

Die Ergebnisse der theoretischen Untersuchungen bildeten die Basis, um das Mehrartenmodell mit Zähldaten von Kleinsäugerarten aus den Waldfragmenten des brasilianischen atlantischen Regenwaldes zu konfrontieren (Kapitel 5). Diese Kalibrierung des Modells führte zu einem besseren Verständnis der strukturbestimmenden Mechanismen dieser hoch diversen und bedrohten Lebensgemeinschaft und zeigte, dass sowohl neutrale als auch nischenbasierte Koexistenzdynamiken wichtig für die Dynamik der Artengemeinschaft sind. Außerdem prognostiziert das parametrisierte Modell eine Zunahme der räumlichen Heterogenität in der Artenzusammensetzung der Kleinsäugergemeinschaft auch wenn der heutige Fragmentierungsgrad der Landschaft sich in Zukunft nicht verschlechtert.

Zusammen tragen die Ergebnisse meiner Doktorarbeit zu einem funktionalen Verständnis derjenigen ökologischen Prozesse bei, die durch inner- und zwischenartliche Konkurrenz entstehen. Die Arbeit zeigt, wie diese ökologischen Prozesse die räumlichen Dynamiken in Populationen und Artengemeinschaften beeinflussen und dazu beitragen, dass verschiedene Arten und Lebensgemeinschaften unterschiedlich auf Umweltwandel reagieren. Im Hinblick auf den Naturschutz verdeutlichen die Ergebnisse potentielle Schwächen üblicher Schutzmaßnahmen und können zukünftige und bisher unbekannte Risiken für das Überleben von Arten und Artengemeinschaften aufdecken.

# General introduction

Anthropogenic environmental change is ubiquitously observed and develops at an unprecedented rate. In this thesis, I focus on two environmental changes that are among the most significant causes of global biodiversity loss: habitat fragmentation and climate change (Sala et al. 2000; Thomas et al. 2004). Potential strategies to mitigate the biodiversity decline depend on robust scientific evidence. However, the extensive temporal and spatial scales of environmental problems hamper the mechanistic understanding of the underlying population dynamics (McCann 2007). Simulation models with explicit descriptions of population processes are well established tools to meet these challenges, but often they focus on single species systems and simple types of intraspecific interactions. Yet, approaches that disregard more complex conspecific and heterospecific interactions are insufficient to provide a deeper ecological understanding of the processes structuring communities (Brooker et al. 2007). Consequently, predicting community responses to fragmentation and climate change are among the biggest challenges ecologists are facing today (Travis 2003).

With this thesis I aim to complement the advances made in theoretical single-species studies by emphasizing species interactions. I examine the effects of different assumptions regarding intra- and interspecific density regulation on single-species persistence, two-species coexistence and multi-species diversity patterns. By asking how density regulation may alter the impacts of habitat fragmentation and climate change, I aim to identify priorities during the development of management plans for populations and communities. I approach these questions using a spatially-explicit process-based simulation model. My approach is twofold: On the one hand, I introduce hypothetical species and analyse basic principles in a virtual environment; on the other hand, I base my analyses on real species observations to test the applicability of the developed model formulations for real communities (Fig. 1).
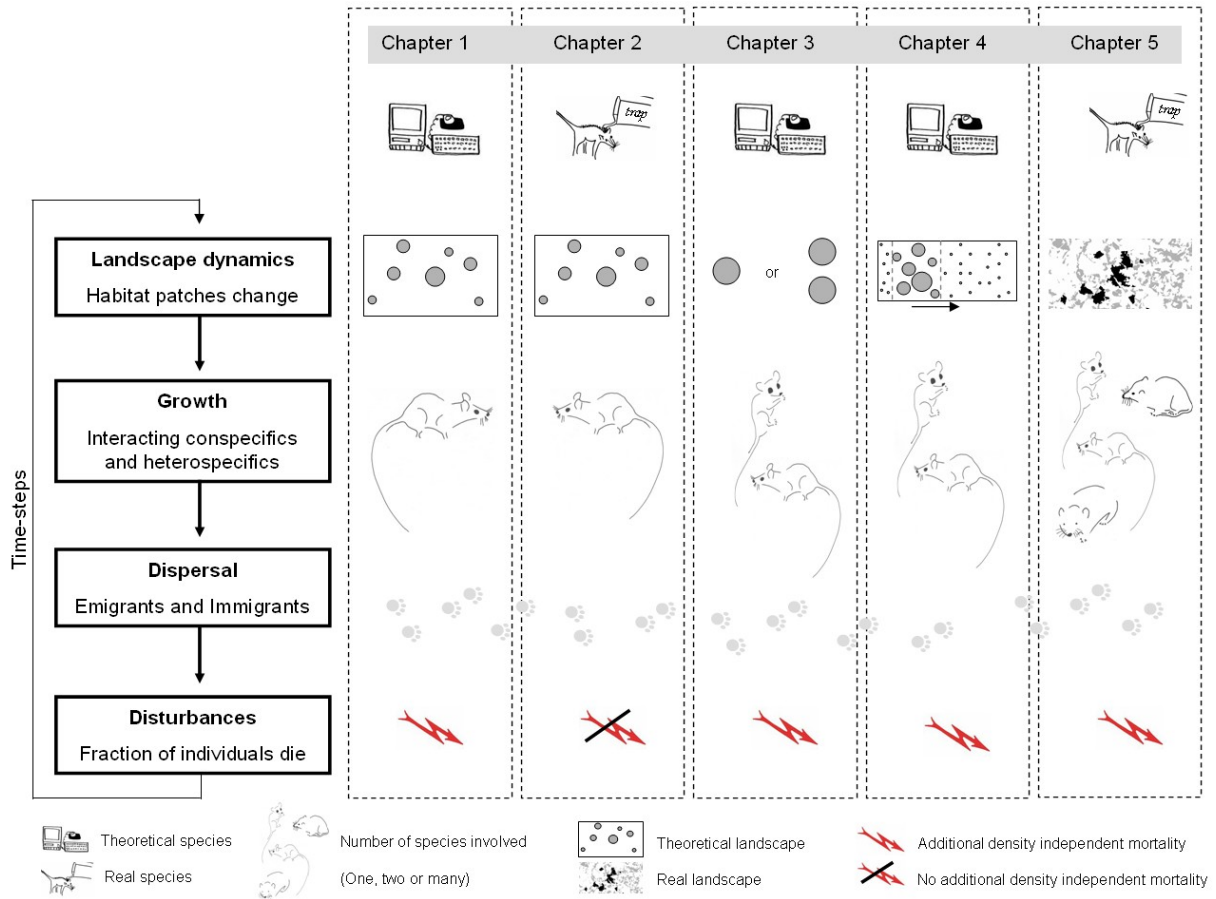
**Figure 1:** Scheme of model complexity and model assumptions across the research chapters. The simulation model is process-based and simulates landscape dynamics, population growth, dispersal and disturbances to identify influences of environmental changes on persistence and coexistence (see process overview on the left). The five research chapters differ in the implementation of the four processes. Most prominent differences are in the number of modelled species, the considered landscape type, whether species are hypothetical or real and whether mortality due to density independent disturbances is considered or not. Dispersal between landscape patches is considered in all chapters.

In this introduction, I briefly re-state essential components of the theory on habitat fragmentation and climate change, review existing information on the mechanisms and strength of density regulation, and highlight the central aspects of my methodological approach. In the first and second core chapters of the thesis, I focus on single-species systems and investigate how intraspecific density regulation (chapter 1) and density independent vs. density dependent dispersal of Tundra voles, *Microtus oeconomus*, (chapter 2) influence spatial synchrony and persistence in fragmented landscapes. In the two subsequent chapters, I analyse interactions within and among two species. I demonstrate that over-compensatory density regulation can promote species coexistence (chapter 3), and examine how climate

change and habitat fragmentation threaten coexistence depending on the underlying coexistence mechanisms (chapter 4). In chapter 5, I use a Bayesian modelling approach to identify potential drivers of small mammal diversity in the fragmented Atlantic forest. The final section synthesizes the findings of this thesis with respect to ecology and conservation, and suggests directions for further research.


## Habitat fragmentation and climate change


Habitat fragmentation and climate change are two of the biggest threats to biodiversity worldwide (Sala et al. 2000; Thomas et al. 2004). Increasing habitat fragmentation during the last decades reduced the habitats of many species to smaller units separated by unsuitable strips of land. In natural systems fragmentation may occur through disturbances like fire, windfall, flooding or soil erosions. However, the most menacing and large-scale cause of habitat fragmentation is the expansion and intensification of human land use (Burgess and Sharpe 1981). Habitat fragmentation forces populations with a formerly continuous spatial distribution into heterogeneous sub-populations occupying the remaining patches of suitable habitat (Hanski and Ovaskainen 2003). As a result, altered demographic stochasticity (random variations in gender ratio, survival probability, mortality and fertility, Hanski 1998), edge effects (higher extinction risks due to changing micro-climatic conditions, Barbosa and Marquet 2002; Taylor et al. 2001) and greater pressure from predators (Lahti 2001) may accelerate extinction. However, the entire set of sub-populations, the 'population of populations', can potentially persist if recolonization outweighs the extinction of sub-populations. This concept of regional persistence depending on colonisation and extinction of subpopulations is typically called the metapopulation concept and was first introduced by Levins (1970). Recolonization depends on connectivity between habitat patches (Gyllenberg and Hanski 1997; Tischendorf and Fahrig 2000b; Johst et al. 2002), determined by species dispersal abilities and landscape structure (Heino and Hanski 2001; Grenfell et al. 1992; Vucetich et al. 2000), and on asynchronous sub-population dynamics, resulting in temporally uncoupled local extinction events (Johst et al. 1999; Murrell et al. 2002; Münkemüller and Johst 2006). Lande (1987) was the first to demonstrate that a critical threshold level of habitat availability exists below which species extinction occurs even though sub-populations still have positive population growth. This threshold is determined by the pattern of habitat destruction, with spatially uncorrelated habitat loss being more severe than correlated loss

(With and King 1999; Hill et al. 1999). On the contrary, habitat fragmentation may even promote species survival via a risk-spreading effect that mitigates impacts of forces such as contagious diseases, fires, or pressure from competitors (Tscharntke et al. 2002). However, these cases are rare and assume spatially uncorrelated environments.

Climate change has produced numerous shifts in the distributions and abundances of species already (Parmesan and Yohe 2003; Thomas et al. 2004), and the prediction of future biogeographic ranges of species is an active area of research. However, most studies utilise correlational approaches to relate current distributions to current climate and then project future distributions onto future climate (Thuiller et al. 2004; Araujo et al. 2004). On their own, these correlational methods are insufficient for predicting future patterns of biodiversity, because they neglect the mechanisms underlying the process of range shifting (Guisan and Thuiller 2005; Heikkinen et al. 2006; Araujo and New 2007). For plants, a number of applied landscape models, such as forest succession and composition models, explicitly consider species interactions and dispersal (Norby et al. 2001; Higgins et al. 2003; Schumacher and Bugmann 2006; Schurr et al. 2007). For animals, few rather specific examples aside, today's literature lacks formal modelling of both the species' abilities to move from currently-suitable to future-suitable areas (for exceptions cf. Best et al. 2007; Travis 2003) and the response of an interacting community to climate change (for exceptions cf. Ferrier and Guisan 2006; Brooker et al. 2007).

## Intra- and interspecific density regulation

So far, most studies investigating species' responses to habitat fragmentation and climate change take a simplified approach disregarding the variety of conspecific and heterospecific competitive interactions prevailing in nature. In single-species approaches, density regulation is often restricted to logistic population growth assuming that the realized per-capita rate of increase decreases linearly with increasing density. However, a substantial body of research provides evidence of nonlinear responses to increasing density (e.g., Godfray et al. 1990; Hastings et al. 1993; Silvertown 1991; Sinha 1997) and suggests that this may significantly impact persistence (e.g., Hastings et al. 1993; Münkemüller and Johst 2006; Damgaard 2007). Moreover, the great majority of work focuses on single species, e.g. by applying viability analyses to flag-ship species. Based on these single-species analyses, ecologists prioritize conservation actions, such as reserve site selection or disturbance reduction, and reason that

other species in the community will be conserved along with the flag-ship species (e.g., Anderson et al. 2007; Chiweshe 2007). Properties of the accompanying species and interactions among them are neglected. However, in reality, competitive interactions within and among species are key drivers of population and community dynamics (Brooker et al. 2007). This thesis demonstrates that a greater understanding of both the different mechanisms of density regulation and the strength of density regulation among heterospecifics is required for a profound understanding of the structure and functioning of communities and for providing unbiased predictions of environmental change effects. Density regulation among heterospecifics will be called interspecific competition in the following.

Mechanisms of density regulation range from over-compensatory via compensatory to under-compensatory regulation (Fig. 2 and 3, May 1975; May 1976; Johst et al. 2008). Over-compensatory regulation (or scramble competition) occurs where resources are spread equally across a number of individuals. At low population sizes this results in high growth rates, but is soon followed by population crashes as the population grows and resources become too thinly spread across the population. Population densities exhibit cyclic or chaotic dynamics over time that can significantly increase local extinction risk (e.g., Allen et al. 1993; Costantino et al. 1997; Ripa and Lundberg 2000). Compensatory regulation (or contest competition) is exhibited where resources are allocated in a one-off contest between competing individuals, and the overuse of resources is avoided. Population densities over time develop towards equilibrium dynamics and fluctuations are only due to stochastic events. Under-compensatory regulation occurs where dynamics are delayed and the adjustment of population sizes to carrying capacities is slow. For instance, storage capacities or complex mating behaviour may lead to a delayed response.

As a rule of thumb, one can expect fluctuations in population sizes and reproduction rates to be large for species that have strong density regulation in early life-stages only, such as insects and fish, intermediate for species with late juvenile and pre-breeding density regulation, and low for large mammals regulating their density at least partly through changes in fertility (Sinclair 1989). However, it is still controversial whether fluctuations observed in nature are caused internally by mechanisms of density regulation or by external forces such as predator-prey dynamics, weather conditions or even the moon cycle (e.g., Tarasov et al. 1998; Lindstrom et al. 2001; Tenow et al. 2007). The main obstacle to the resolution of this controversy is the difficulty of determining the mechanisms of density regulation from field data (Godfray et al. 1990; Morris 1990). Estimates depend on long-term and high-quality time-series from which the information on frequency, amplitudes and intervals of fluctuations

can be estimated. Unfortunately, such time-series are rare. Furthermore, it is most often impossible to unambiguously assign fluctuations to their causes as a large body of processes (i.e. stochasticity, dispersal, competition, predator-prey interactions in food webs or differential uptake rates of multiple and possibly fluctuating resources) mutually 'dilutes' causal relations (Sinha 1997; Newey et al. 2007). Even for time-series produced by simulation models it is difficult to identify the mechanism of density regulation without an *a priori* knowledge of all processes included in the model (Fig. 2).
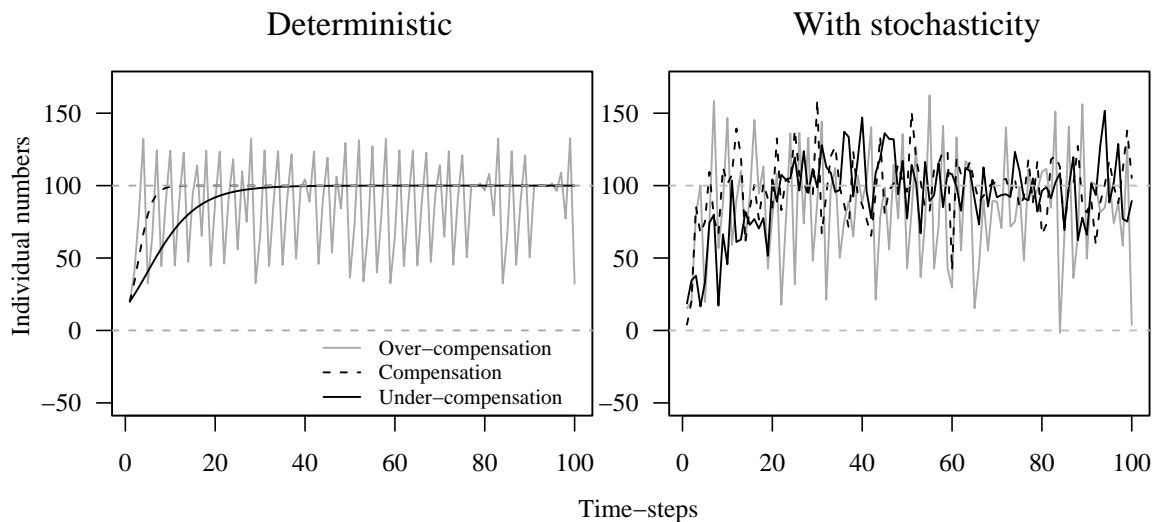


**Figure 2:** Time-series of over-compensating, compensating and under-compensating population dynamics under deterministic vs. highly stochastic conditions. Horizontal dashed lines mark extinction threshold and carrying capacity (Carrying capacity = 100; Maximum growth rate = 2; Parameter for mechanism of density regulation = 0.3, 1 or 7, cf. section 'Modelling the dynamics of populations'). In the plot with stochasticity a normally distributed random effect (with $\mu = 0$ and $\sigma = 20$) is added.

Nevertheless, there is considerable evidence of a range of density regulation mechanisms operating under experimental and 'natural' conditions including cyclic fluctuations and chaos, as they could emerge from over-compensatory density regulation (Godfray et al. 1990; Hastings et al. 1993). Among the possible examples for over-compensation are butterflies (*Tyria jacobaeae*, Vandermeijden et al. 1991), beetles (*Dendroctonus frontalis*, Reeve et al. 1998; *Hadramphus spinipennis*, Schöps 2002), and small mammals (*Arvicola terrestris*, Aars et al. 2001; *Microtus ochrogaster*, Getz et al. 2006). The role of over-compensation in plant population dynamics remains open to question (Damgaard and Borksted 2004; Damgaard

2007). Most notable, both field and theoretical ecologists have suggested that different mechanisms of density regulation may influence population and community dynamics differently and should thus be considered in more detail in population and community studies (Hastings et al. 1993; Lundberg et al. 2000; Murrell et al. 2002; Münkemüller and Johst 2006; Best et al. 2007).
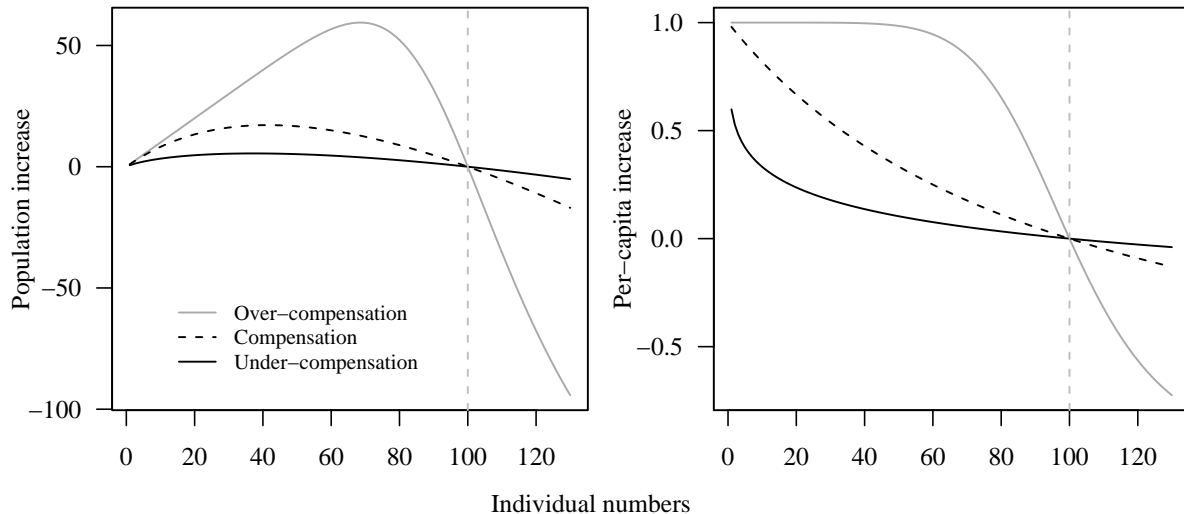


**Figure 3:** Changes in population size and realized per-capita rate of increase between consecutive time steps for over-compensating, compensating and under-compensating density regulation; Dashed vertical lines mark carrying capacity (Carrying capacity = 100; Maximum growth rate = 2; Parameter for mechanism of density regulation = 0.3, 1 or 7, cf. section 'Modelling the dynamics of populations')

Where resource demands overlap, density regulation occurs not only within but also between species, and competitors constrain each other in reproduction, growth, and ultimately persistence. Competition can be demonstrated via its effect on the competitors, e.g. as competitive release in the absence of competition (Abramsky and Sellah 1982) and as competitive displacement of species when competition is intense (Davidson 1978). The strength of competition depends on the degree of resource overlap. Where the overlap is complete and species share exactly the same ecological niche, the strength of density regulation between heterospecifics equals regulation between conspecifics. For this case, experimental work on *Paramecium* species has revealed that species are not able to coexist (Gause 1934). The species that can persist at the lowest level of resource availability is the best competitor and is predicted to exclude the other (Tilman 1982). This 'principle of

competitive exclusion' appeared as one of the first 'laws' in ecology (Barot 2004) and was well complemented by theoretical work stating that intraspecific competition must be greater than interspecific competition to promote coexistence, i.e. coexistence is only possible under resource partitioning (Lotka 1925; Volterra 1926). Pointing to the apparent contradiction between the 'principle of competitive exclusion' and observations of many highly diverse natural communities existing on a low number of resources, Hutchinson (1961) raised the 'paradox of the plankton'. This paradox can be solved by revisiting the large number of homogeneity assumptions that are linked to the 'principle of competitive exclusion' and greatly limit possible competitive outcomes. Relaxing these assumptions opens a suite of possible explanations for coexistence on a low number of resources (Levins 1970; Chesson 1985; Chesson 2000a; Huisman et al. 2001; Huisman and Weissing 2002; Barot 2004). Chesson (1994; 2000b) classified these explanations in 'equalizing' and 'stabilizing' coexistence mechanisms.

Equalizing coexistence mechanisms build on minimizing the differences in average fitness of the coexisting populations (e.g. Hubbell 2001; Etienne and Olff 2005; Latimer et al. 2005; Walker 2007; Hubbell 2006; Rosindell and Cornell 2007). On the contrary, stabilizing coexistence mechanisms rely on increased intraspecific competition strength compared to interspecific competition strength which disproportionally reduces the average fitness of the more abundant species. Among the stabilizing coexistence mechanisms, some depend on heterogeneous distributions of species in space (i.e. spatial storage effects, Shmida and Ellner 1984; Hanski and Woiwod 1993; Chesson 2000a; Durrett and Levin 1998; Neuhauser and Pacala 1999). Others depend on fluctuations of population densities in time and, therefore, can foster coexistence via temporal storage effects or via different nonlinear responses to common fluctuating abiotic or biotic limiting factors (Chesson 1994; Chesson 2003).

## Modelling population and community dynamics

The development of policies to prevent or mitigate the impacts of environmental change on species communities requires a mechanistic understanding of spatial population and community dynamics on large temporal and spatial scales. At large scales, species persistence and coexistence processes are not easily amenable to field experiments, but process-based simulation models are well established and offer a powerful approach to these questions.

Four demographic processes determine the dynamics of populations: birth, death, immigration and emigration. This 'fact of life' (Begon et al. 1996) also guides the process-oriented approach of the time-discrete model developed here (Fig. 1): The growth process involves density dependent birth and death, the dispersal process determines emigration and immigration and the disturbance process adds density independent death. The model considers a landscape represented as a rectangular grid with habitat patches that are surrounded by matrix (i.e., non-habitat) cells. To model the effects of environmental changes, habitat patches may vary in size and connectivity, go extinct and regrow, or follow a 'climate change window' moving from one side of the grid to the other (Travis 2003; Best et al. 2007). To illustrate the role of density regulation in the model, the growth function will be explained in more detail in the following paragraph.

A number of functions have been used to describe growth processes that include a range of potential density regulation mechanisms (cf. Bellows 1981). Here, an extended version of the Maynard Smith – Slatkin equation (1973; see also Hassell and Comins 1976) was selected (For the analyses of single-species persistence, chapter 1 and 2, and two-species coexistence, chapter 3, I additionally tested further density regulation functions but found that qualitative results did not depend on model choice.):

$$N_{s,i}(t+1) = \frac{N_{s,i}(t) \cdot R_s}{1 + (R_s - 1)\left(\frac{N_{tot,s,i}(t)}{CC_{i,s}(t)}\right)^{b_s}}$$

$N_{s,i}(t)$ is the population size of species $s$ on patch $i$ at time-step $t$, $R_s$ is the maximum growth rate of species $s$, which is close to the realized growth rate when individual numbers are far below carrying capacity. The mechanism of density regulation is determined by the parameter $b$: a value below one corresponds to under-compensating density regulation, a value equal to one corresponds to compensating density regulation, and a value above one corresponds to over-compensating density regulation. In a single species system, $N_{tot,s,i}(t)$ equals $N_{s,i}(t)$ and growth is limited by the mechanism of density regulation, $b$, the local carrying capacity, $CC_i$, and the local density, $N_{s,i}(t)$.

In a multi-species approach, the growth rate of each species $s$ is additionally limited by the overall competition pressure from all other species on the patch that is determined by the weighted total number of individuals from all $q$ species living on the patch, $N_{tot,s,i}(t)$:

$$N_{tot,s,i}(t) = \sum_{p=1}^{q} a_{ps} N_{i,p}(t)$$

The weighting factor $a_{ps}$ describes the strength of competition between species $p$ and $s$: A value equal to zero corresponds to a lack of competition, and a value of one corresponds to interspecific competition being as strong as intraspecific competition, because intraspecific competition is set to one. The extended Maynard Smith – Slatkin equation (Maynard Smith and Slatkin 1973) relates very well to the focus of my research because it offers the possibility to model single- and multi-species systems and to vary the mechanisms of density regulation (via parameter $b$) and the strength of competition (via parameter $a$) independently. The mechanisms of density regulation range from over- to under-compensation, and their strength can be assessed by comparing density regulation between and within species.

The following chapters seek to understand whether and how different assumptions of intra- and interspecific density regulation influence single-species persistence, two-species coexistence and multi-species diversity patterns. Each of the subsequent chapters uses a subset of possibilities to vary the mechanisms and strength of density regulation (Fig. 1). Chapter 1 explores the effects of the different mechanisms of density regulation, ranging from strong under-compensation to strong over-compensation, on spatial synchrony and persistence in a single-species system. The study highlights that peaks of spatial synchrony do not only occur at over-compensatory but also at under-compensatory density regulation while increasing extinction risks appear only at over-compensatory density regulation. Chapter 2 scrutinises recent findings on a desynchronising effect of negatively density dependent dispersal (Ims and Andreassen 2005) and demonstrates that strong synchrony may nevertheless emerge from negatively density dependent dispersal if emigration rates are sufficiently high and density regulation is over-compensatory. Chapter 3 investigates the coexistence of two species with equal intra- and interspecific density regulation strength and finds that coexistence is possible if species differ in their density regulation mechanisms and at least one species exhibits over-compensation. Chapter 4 evaluates two ways to coexistence that emerge from different combinations of density regulation mechanisms: neutral

coexistence for species with identical density regulation and coexistence through over-compensation for species with different density regulation. The study demonstrates that the impacts of patch isolation and climatic range-shifting on coexistence differ depending on the underlying coexistence mechanisms. Chapter 5 broadens the approach to a multi-species community and investigates diversity patterns for neotropical small mammals in the Atlantic forest of Brazil. The results show that interspecific competitive interactions comprise both neutral and niche-based coexistence dynamics, and that they are highly relevant for shaping community structure.

# 1 How does intraspecific density regulation influence metapopulation synchrony and persistence? [1]

Intraspecific density regulation influences the synchronisation of local population dynamics through dispersal. Spatial synchrony in turn may jeopardize metapopulation persistence. Joining results from previous studies suggests that spatial synchrony is highest at moderate over-compensation and is low at compensating and at very strong over-compensating density regulation.

We scrutinise this supposition of a unimodal relationship using a process-based metapopulation model with explicit local population dynamics. We extend the usually studied range of density regulation to under-compensation and analyse resulting metapopulation persistence. We find peaks of spatial synchrony not only at over-compensatory but also at under-compensatory density regulation and show that effects of local density compensation on synchrony follow a bimodal rather than unimodal relationship. Persistence of metapopulations however, shows a unimodal relationship with a broad plateau of high persistence from compensatory to over-compensatory density regulation. This range of high persistence comprises both levels of low and high spatial synchrony. Thus, not synchrony alone jeopardizes metapopulation persistence, but only in interplay with high local extinction risk. The functional forms of the relations of density compensation with spatial synchrony and persistence are robust to increases in dispersal mortality, landscape dynamics, or density dependence of dispersal. However, with each of these increases the maxima of spatial synchrony and persistence shift to higher over-compensation and levels of synchrony are reduced.

Overall, for over-compensation high landscape connectivity has negative effects while for under-compensation connectivity affects persistence positively. This emphasizes the importance of species life history traits for management decisions with regard to landscape connectivity: While dispersal corridors are essential for species with under-compensatory

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density regulation, they may have detrimental effects for endangered species with over-compensation.

## 1.1 Introduction

In metapopulation networks dispersal facilitates the spreading of extinction risks. However, risk spreading only works if the local population dynamics in the metapopulation are not fully synchronized (DenBoer 1968). High degrees of synchrony accelerate metapopulation extinction. This has been shown not only in theoretical (e.g. Heino et al. 1997; Petchey et al. 1997; Matter 2001; Murrell et al. 2002) but also in empirical studies (e.g. Sutcliffe et al. 1996; Forare and Solbreck 1997; Koenig 1998; Moilanen et al. 1998; Harrison et al. 2000; Sherratt et al. 2000; Johst and Schöps 2003). Accordingly, analyzing the causes and impacts of synchrony between local population dynamics (called spatial synchrony in the following) on metapopulation dynamics gained much attention in the past decades (e.g. Ranta et al. 1995; Heino et al. 1997; Ruxton et al. 1997; Kaitala and Ranta 1998; Ranta et al. 1999; Ripa and Lundberg 2000; Buonaccorsi et al. 2001; Murrell et al. 2002). Moran (1953) was the first to suggest that spatially correlated processes may cause spatial synchrony. Today, these correlated processes are commonly interpreted as global disturbances affecting the entire metapopulation at once (Ranta et al. 1999). Even though the 'Moran effect' is well confirmed in theoretical (e.g. Ranta et al. 1995; Heino et al. 1997; Haydon and Steen 1997; Lambin et al. 1998) as well as in empirical studies (e.g. Hanski and Woiwod 1993; Lindström et al. 1996; Bjørnstad et al. 1999; Ranta et al. 1999), it does not explain another commonly observed pattern among synchronized local populations: a negative correlation between spatial synchrony and distance between patches independent of any local disturbances (Hanski and Woiwod 1993; Ranta et al. 1995; Lindström et al. 1996; Koenig 1999). This second type of synchrony is commonly explained by dispersal (Ranta et al. 1995; Ranta et al. 1997; Heino et al. 1997; Kaitala and Ranta 1998; Lambin et al. 1998). Hence, two major causes for spatial synchrony in single species systems were detected: auto-correlated disturbances and dispersal. In the present chapter the latter will be analyzed in more detail.

The mode of intraspecific density regulation is critical for its effects on spatial synchrony (Allen et al. 1993; Heino et al. 1997; Bjørnstad 2000; Kendall et al. 2000; Ripa and Lundberg 2000; Ripa and Lundberg 2000; Silva et al. 2000; Matter 2001; Murrell et al. 2002). We will distinguish between three intergradient modes in the following: (1) Over-compensatory

density regulation leads to population dynamics with un-damped oscillations or chaos (unstable dynamics, May 1974; Allen et al. 1993; Costantino et al. 1997; Ripa and Lundberg 2000). Peaks and crashes are frequent and enhance the extinction risk of populations (Allen et al. 1993; Costantino et al. 1997; Ripa and Lundberg 2000). Scrambling for coveted resources is a behavioural example that typically entails over-compensatory density regulation. (2) Compensatory density regulation leads to the adjustment of local population sizes to carrying capacities over time. Densities fluctuate only due to environmental influences (monotone convergence). Territorial behaviour and pecking orders are behavioural examples that effectively lead to the avoidance of over-using resources and thus to compensatory density regulation. (3) Under-compensatory density regulation leads to a weak influence of resources (e.g. due to storage capacities) on population growth rate and thus to a slowed adjustment of population sizes to carrying capacities over time. Yet, empirical support for under-compensation is rare (cf. Jarosik and Dixon 1999), and it has only rarely been investigated in theoretical studies (cf. Petchey et al. 1997).

According to Ripa (2000), dispersal is only an effective synchronizing mechanism when local dynamics are close to unstable (moderate over-compensation). Thus, synchrony increases with increasing population growth rate (Hanski and Woiwod 1993; Lundberg et al. 2002) and instability of local dynamics (Ripa and Lundberg 2000; Bjørnstad 2000; Kendall et al. 2000). Yet, Parthasarathy and Güemez (1998) found that already a small heterogeneity in population growth rates can disrupt otherwise synchronous dynamics. Furthermore, even under spatially correlated noise (Moran effect), increasing growth rates may cause asynchronous chaotic dynamics (Heino et al. 1997; Matter 2001). These results suggest a de-correlating effect of locally chaotic dynamics (Allen et al. 1993; Kendall et al. 2000). In sum, based on the existing literature we would expect a unimodal relation with a peak of spatial synchrony at moderate over-compensation (Bjørnstad 2000; Kendall et al. 2000). However, we still lack both an investigation of under-compensatory density regulation as well as a systematic analysis over the whole range of possible modes of local density regulation.

Besides density regulation, dispersal traits and landscape structure influence the synchronization of local population dynamics through dispersal and thereby might change the role of density regulation in spatial synchrony (e.g. Matter 2001). High emigration rates and long dispersal distances are synchronizing forces as they increase connectivity between patches (e.g. Hanski and Woiwod 1993; Bascompte and Solé 1995; Ranta et al. 1995; Ripa and Lundberg 2000; Buonaccorsi et al. 2001; Johst and Schöps 2003; Murrell et al. 2002) whereas dispersal mortality and landscape dynamics are de-synchronizing forces (e.g. Ruxton

et al. 1997; Münkemüller and Johst 2006). Local environmental noise or heterogeneity in resource availability can reduce synchrony as well (Bascompte and Solé 1995; Heino et al. 1997; Petchey et al. 1997; Matter 2001).

We provide a systematic analysis of the influence of density regulation, over its entire range from under-compensation to strong over-compensation, on spatial synchrony. Thereby, we unify earlier findings on the role of compensatory and over-compensatory density regulation with new ones on the role of under-compensatory density regulation. We then test the robustness of the found relation with respect to dispersal mortality, density dependent dispersal, and landscape dynamics (patch destruction and regeneration). Finally, we compare the level of spatial synchrony with resulting metapopulation persistence.

## 1.2 Model description

### *Model description*

We analysed the influences of different modes of local density regulation on spatial synchrony and metapopulation persistence with an extended version of the metapopulation model by Münkemüller and Johst (2006). The key processes in the model occurred in the following order: landscape dynamics, local population growth, and dispersal (cf. appendix Fig. 1.6, Tab. 1.1).

The landscape was represented by a grid of 20 * 20 cells with 10 randomly distributed habitat patches. Maximum carrying capacities, $K_{i,max}$, of each patch were drawn randomly from a uniform distribution with a range of 50 to 150 individuals and were set as initial carrying capacities. According to landscape dynamics, patches were put at risk of being destroyed at each time step (patch destruction with certain probabilities). Such local extinction events were followed by setting current carrying capacities, $K_i(t)$, to 1 and population sizes to 0 (local populations go extinct). In the following time steps, patches and carrying capacities recovered with a reproduction rate equal to the Eulerian number, $e$, and according to the equation of Maynard Smith and Slatkin (Maynard Smith and Slatkin 1973, equation 1.1). Dispersers can recolonize these re-growing patches (if $K_i(t)>1$).

$$K_i(t+1) = K_i(t) * e \big/ \big(1 + (e-1)\big(K_i(t)/K_{i,\max}\big)\big) \qquad (1.1)$$

Local populations were initialized randomly from a uniform distribution between 10 individuals and the maximum carrying capacities of the corresponding patches. Local population dynamics were described by the equation of Maynard Smith and Slatkin (1973):

$$N_i(t+1) = N_i(t) * R_i \Big/ \Big(1 + (R_{base} - 1)(N_i(t)/K_i)^b\Big), \tag{1.2}$$

where $R_i(t)$ describes population growth without competition, and $b$ characterizes the mode of density dependence ($b < 1$ corresponds to under-compensating, $b = 1$ to compensating, and $b > 1$ to increasingly strong over-compensating density regulation). To include environmental stochasticity, $R_i(t)$ fluctuated randomly and uniformly between 0 and $0.8 * R_{base}$ in each time step. For our simulations, $R_{base}$ was always set to 15. Thereby, we simulated the full range of density regulation from under-compensation to strong over-compensation. To include demographic stochasticity, we used integer individual numbers and drew the actual local population sizes from a Poisson distribution with mean $N_i(t+1)$. When the population size reached a lower bound of less than two individuals, the population was assumed to be extinct due to the Allee effect (Allee 1931, this assumption has negligible effects on the results). The only possibility of the population being reactivated was by recolonization through dispersal.

The dispersal strategy was determined by different dispersal traits. We used high emigration probabilities ranging from 0.65 to 0.75 (equally distributed) and long-range dispersal (the mean dispersal distance in our simulations equalled the mean distance between the randomly located patches in the grid, mean $D_d = 10.32$ grid cells), as several studies have shown that these conditions favour synchronisation (Hanski and Woiwod 1993; Ranta et al. 1995; Ripa and Lundberg 2000; Murrell et al. 2002). Emigration probabilities for each patch $i$, $P_{e,i}(t)$, were determined by the following equation:

$$P_{e,i}(t) = \min\Big(v(N_i(t)/K_i(t))^w, 0.9\Big), \tag{1.3}$$

where $v$ determines the amount of emigrants while $w$ determines its density dependence i.e. dependence on the ratio between the population size and the carrying capacity ($w = 0$ corresponds to density independent emigration, $w = 1$ corresponds to linear (positive) density dependence, and $w > 1$ corresponds to smaller proportions of emigrants for $K_i(t) > N_i(t)$).

We analysed different forms of density dependent emigration by varying $w$. For each of these scenarios we ran different simulations with $v$ values ranging from 0 to $3*10^8$, and

calculated the effective mean emigration probabilities over years and local populations from the simulation outputs. From all these simulations we selected those with calculated emigration probabilities ranging from 0.65 to 0.75, the same range of values we used for emigration probabilities in the simulation scenarios with density independent emigration ($w = 0$). Thus, results include metapopulations that were comparable in their mean emigration probabilities but showed high spatial and temporal variability. The number of emigrants per patch was drawn from a binomial distribution with the parameters $P_{e,i}(t)$ and $N_i(t)$. Emigrants from patches $i$ were allocated to patches $j$ ($i \neq j$) using a matrix of transfer probabilities, $P_{ij}$, with values decreasing exponentially with distance, $D_{ij}$:

$$P_{ij} = \exp\left(-\frac{1}{D_d}D_{ij}\right)\bigg/ \sum_j \exp\left(-\frac{1}{D_d}D_{ij}\right) \times P_s \qquad (1.4)$$

The survival probability during dispersal, $P_s$, was assumed to be linearly distance-dependent. For a distance of 0 cells probability of survival was set to 1. The number of immigrants per patch was drawn from a multinomial distribution parameterized via the transfer probabilities $P_{ij}$, dispersal mortality probabilities $P_{i,death}$ (equation 1.5) and the number of emigrants.

$$P_{i,death} = 1 - \sum_j P_{ij} . \qquad (1.5)$$

Consequently, the sum of immigrants and dying dispersers equalled the sum of emigrants (closed system).

### *Simulation experiments and evaluation*

In our simulation experiments we varied the mode of intraspecific competition from under-compensatory to over-compensatory density regulation ($ln(b) = [-2.7, 2.5]$) and analysed the effects on spatial synchrony and metapopulation persistence (100 time steps and 100 simulation runs for each parameter combination). To better understand the resulting relationships, we also monitored the mean and variance of the local population sizes as well as the local extinction risk. We repeated the entire analyses for increasing dispersal mortality (for a distance of 50, 25, 17, 12.5 or 10 cells the probability of survival was set to 0), landscape dynamics (probability of patch destruction per time step was set to 0, 0.05, 0.1,

0.15, 0.2; Fig. 1.2) and increasingly density dependent dispersal (w = 0, 1, 5; Fig. 1.3; cf. appendix Tab. 1.1).

Synchronization was determined by mean cross-correlation coefficients. The mean cross correlation was based upon the Pearson product-moment correlation of the differences in local abundances between years (called Pearson $\Delta N$ unless otherwise noted). We used this coefficient to account for both the correlation of the directions of changes (Buonaccorsi et al. 2001; Liebhold et al. 2004) and the correlation of the magnitude of these changes. In order to demonstrate the effect of the chosen correlation coefficient, we additionally computed a modified version of Kendall's $\tau$ (Buonaccorsi et al. 2001; Liebhold et al. 2004) and the Pearson product-moment correlation of the local abundances (called Pearson $N$) for a basic scenario (density independent dispersal without dispersal mortality in non-dynamic landscapes).

τ = 2 * (number of points in time local populations move in the same direction) / (number of points in time local populations are both alive) – 1　　　　　　　　　　　　　(1.6)

The fraction term in equation 1.6 equals the average fraction of time (over all patches) that pairs of series agree about the directions of changes (Buonaccorsi et al. 2001). As a measure of metapopulation persistence, we determined the probability of metapopulation survival for a 100 year time span.

The simulation model was implemented with the Borland C++ Builder 5, numerical routines from the GNU Scientific Library (http://sources.redhat.com/gsl/ref/gsl-ref_toc.html) were used for the probability distributions and graphics were generated in R 2.2.0 (R Development Core Team 2005).

## 1.3 Results

In our analysis we considered the effects of local density regulation on (1) mean local population sizes, (2) their variability, (3) mean number of local extinction events, (4) spatial synchrony and (5) metapopulation persistence.
(1) Mean local population size increases with increasing strength of density compensation (rising values of b; Fig. 1.1a). (2) The mean temporal variability in local population sizes is highest with under-compensation and over-compensation, but low in-between (Fig. 1.1b).
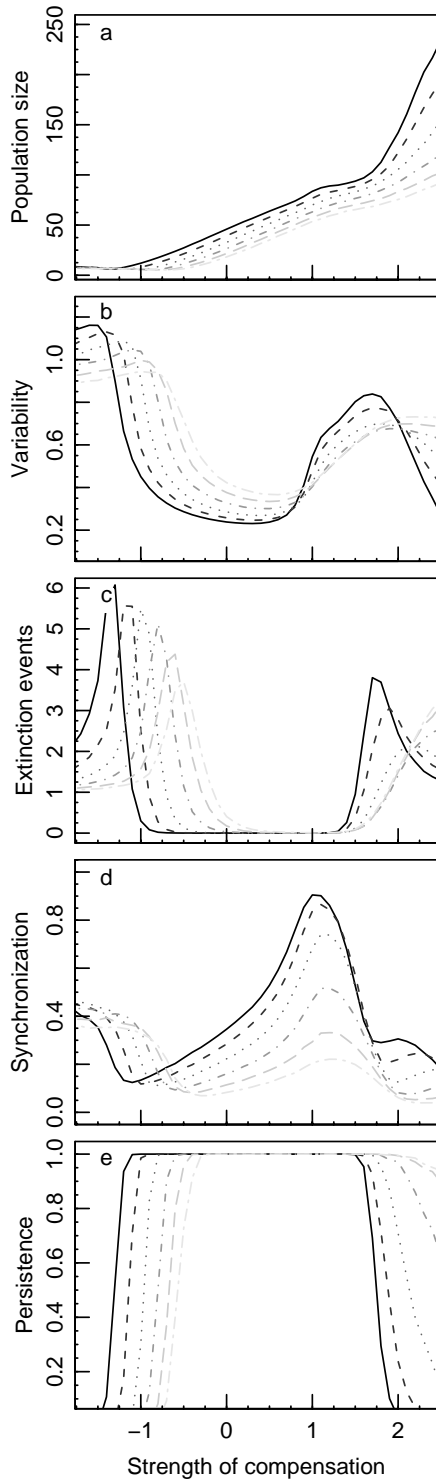
**Figure 1.1:** Impact of density regulation on (a) the mean population size, (b) the mean variability of local populations, (c) the mean number of local extinction events per 100 years, (d) the synchronization of local population sizes, and (e) metapopulation persistence. Decreasing grey level of lines illustrates increasing dispersal mortality (Density regulation, *ln(b)*, on the abscissa: negative values correspond to under-compensation, 0 corresponds to compensation, and positive values correspond to over-compensation; solid line: no mortality, shortly dashed line: all dispersers die when dispersing 50 cells on average, dotted line: 25 cells, dot and short dash line: 17 cells, longish dashed line: 12.5 cells, dot and long dash line: 10 cells).

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For very strong over-compensation, low variability of densities is caused by extremely high local extinction risks and resulting low densities and number of occupied patches. (3) The mean number of local extinction events in principle follows the variability of the local population sizes and is highest with under-compensation and high over-compensation (Fig. 1.1c). For very high over-compensation, the total number of local extinction events is low again. Even if patches go extinct regularly this number is low due to the low number of occupied patches (extinction can only occur in occupied patches). (4) The mode of density regulation has a strong effect on spatial synchrony (Fig. 1.1d). Synchrony has two peaks: a moderate one at strong under-compensatory density regulation (max = 0.4) and a high one at over-compensatory density regulation (max = 0.9). Note that the second peak of synchrony coincides with a low local extinction risk (Fig. 1.1c). (5) Persistence is low for both under-compensatory and strongly over-compensatory density regulation and high in-between (Fig. 1.1e).
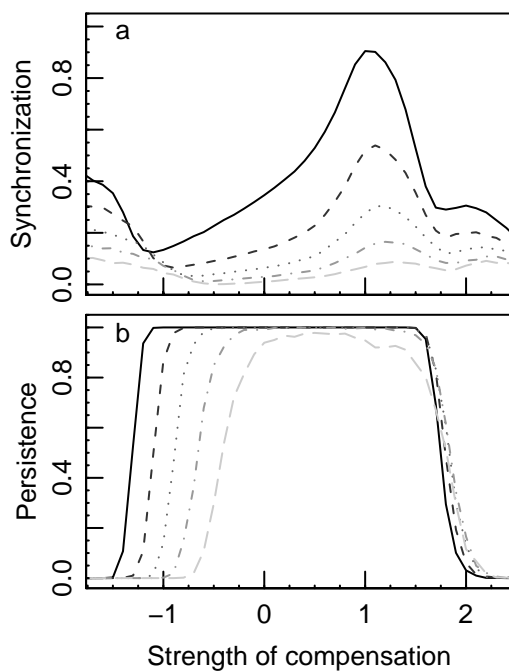


**Figure 1.2:** Impact of density regulation on (a) the synchronization of local population sizes and on (b) metapopulation persistence. Decreasing grey level of lines illustrates increasingly frequent patch destruction (Density regulation, *ln(b)*, on the abscissa: negative values correspond to under-compensation, 0 corresponds to compensation, and positive values correspond to over-compensation; solid line: no patch destruction, shortly dashed line: patch destruction probability of 5%, dotted line: 10%, longish dashed line: 15%, dot and long dash line: 20%).

Increasing dispersal mortality does not change the general functional forms of the discussed relationships but affects their position. The increase in local population sizes with increasing strength of density compensation is lower (Fig. 1.1a). Effects on the two maxima of the variability of local density, the number of local extinction events and the synchronization are twofold (Fig. 1.1b, c, d): (1) maxima only occur at stronger density compensation (shift of the maxima to the right along the abscissa, e.g. for synchrony from $b =$ 2.7 without dispersal mortality to $b = 3.3$ with high mortality); (2) values of maxima are reduced (shift of the maxima downwards, e.g. for synchrony from 0.9 to 0.2). For metapopulation persistence, a shift of the curve towards over-compensatory density regulation occurs (shift to the right), i.e. a better persistence with higher dispersal mortality for over-compensatory density regulation and a reduced persistence for under-compensatory density regulation (Fig. 1.1e).
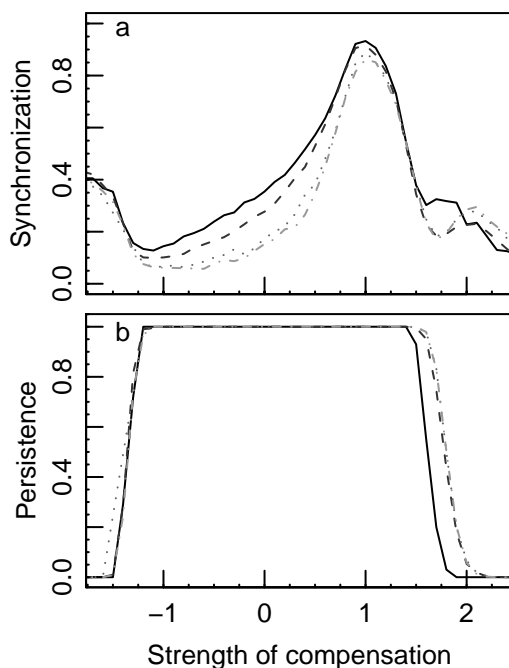


**Figure 1.3:** Impact of density regulation on (a) the synchronization of local population sizes and on (b) metapopulation persistence. Decreasing grey level of lines illustrates increasingly strong density dependency of emigration (Density regulation, *ln(b)*, on the abscissa: negative values correspond to under-compensation, 0 corresponds to compensation, and positive values correspond to over-compensation; solid line: no density dependence, w = 0 -see equation 1.3 in the method section-, shortly dashed line: linear (positive) density dependence, w = 1, dotted line: w = 3, longish dashed line: w = 5).

We repeated the entire analyses for increasing landscape dynamics and increasingly density dependent dispersal. As their effects are very similar to that of increasing dispersal mortality, we only visualise the results for spatial synchrony (Fig. 1.2a, Fig. 1.3a) and metapopulation persistence (Fig. 1.2b, Fig. 1.3b). Again, the synchronisation curve shifts to larger *b* and lower synchronisation levels. The metapopulation persistence curve generally shifts to stronger density compensation (larger values of *b*). Density dependent dispersal or increased landscape dynamics reduce metapopulation persistence at under-compensation and slightly enhance it at over-compensation.
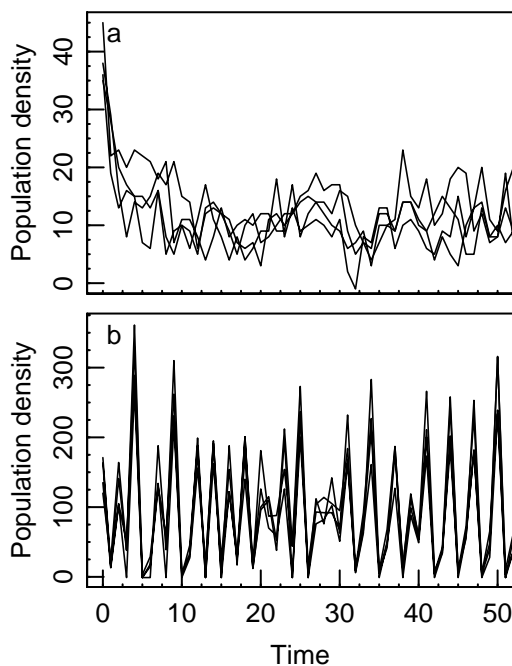


**Figure 1.4:** Development of four randomly chosen local population densities (out of ten) over the first 50 time steps for (a) under-compensation with *ln(b)* = -1 and (b) moderate over-compensation with *ln(b)* = 1.5 in a basic scenario (density independent dispersal without dispersal mortality in non-dynamic landscapes).

A time-series of local population densities (basic scenario: density independent dispersal without dispersal mortality in non-dynamic landscapes) exemplifies contrasts between two density regulation types resulting in low and high synchrony (Fig. 1.4). For under-compensation dispersal is not able to synchronize population fluctuations and the influence of environmental stochasticity is high (Fig. 1.4a) whereas for moderate over-compensation dispersal can synchronize local populations despite environmental stochasticity (Fig. 1.4b). For under-compensation, population densities decrease to a quite low level during the first

time steps (Fig. 1.4a). This is due to assumed environmental stochasticity and does not occur for constant reproduction rates (results not shown).
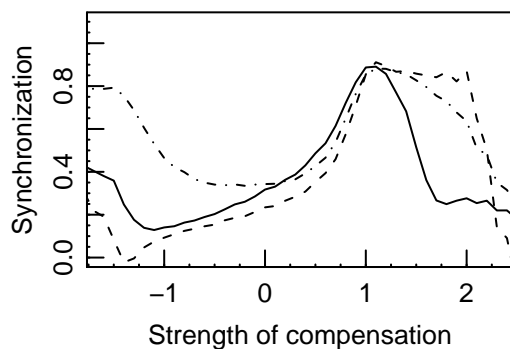


**Figure 1.5:** Impact of different cross correlation coefficients on the results in a basic scenario (density independent dispersal without dispersal mortality in non-dynamic landscapes); solid line: Pearson correlation coefficient of differences in local abundances (Pearson $\Delta N$), shortly dashed line: a modified version of Kendall's $\tau$, and longish dashed line: Pearson correlation of local abundances (Pearson $N$).

Comparing three possible measures of synchrony (Pearson $N$, Pearson $\Delta N$ and Kendall's $\tau$; basic scenario) reveals that they are similar around compensatory density regulation but differ at under- and over-compensatory density regulation (Fig. 1.5). For under-compensation Kendall's $\tau$ is lowest followed by Pearson $\Delta N$ and Pearson $N$ whereas for over-compensation Pearson $\Delta N$ is lowest followed by Pearson $N$ and Kendall's $\tau$.

## 1.4 Discussion

Spatial synchrony is a severe threat to metapopulation persistence and is thus a topic of continuing debate (Ranta et al. 1995; Ranta et al. 1997; Heino et al. 1997; Kaitala and Ranta 1998; Lambin et al. 1998). This study contributes by analysing the role of local density regulation in this process and by comparing synchronization with resulting metapopulation persistence.

### Shape of the relation between the mode of density regulation and spatial synchrony

Our results summarize earlier findings on spatial synchrony in the range of compensatory to over-compensatory density regulation: synchrony is low for compensation (cf. Kendall et al. 2000; Ashwin 2003) and strong over-compensation (Allen et al. 1993; Kendall et al. 2000; Ripa and Lundberg 2000; Silva et al. 2000) but high in-between (Hanski and Woiwod 1993; Ripa and Lundberg 2000). We expanded this already quite well investigated range of density regulation towards under-compensation and found a previously unknown second peak of spatial synchrony (Fig. 2.1d). This second peak is even more pronounced in models which describe environmental stochasticity via random fluctuations of the carrying capacity instead of the reproductive rate (results not shown) and for synchrony measurements which account for the absolute values of population densities (Pearson $N$) and not only for changes in these densities (Pearson $\Delta N$ and Kendall's $\tau$; Fig. 1.5).

The two peaks of spatial synchrony at under-compensation and over-compensation result from two different mechanisms: (1) For under-compensation, adjusting local densities via dispersal to similar sizes is easy. Intrinsic regulating forces are too weak to counteract this adjustment (slow convergence towards carrying capacities). Thus, dispersal is sufficient to produce high synchrony of local population densities (i.e. Pearson $N$) and moderate synchrony of changes in local population densities (i.e. Pearson $\Delta N$ and Kendall's $\tau$; Fig. 1.5). (2) For over-compensation, adjusting local densities to similar sizes is not sufficient to cause synchrony since strong regulating forces (strong convergence towards carrying capacities, cycles or chaos) immediately counteract. Instead, it is necessary to superimpose these intrinsic regulating forces, such that they are in phase with each other. This mechanism is able to generate high synchrony at moderate over-compensation (cycles, cf. Fig. 1.4b). However, it fails in cases where intrinsic regulating forces have different directions, e.g. pull densities to different carrying capacities (compensation), or show completely irregular patterns (chaotic dynamics at strong over-compensation).

### Robustness of the relation between the mode of density regulation and spatial synchrony

The robustness of the bimodal relationship between spatial synchrony and the mode of local density regulation was tested for species with different dispersal abilities (increasingly high dispersal mortality and increasing density dependence of dispersal) and for dynamic landscapes (increasingly frequent patch destruction and regeneration).

Increasing dispersal mortality results in reduced local population densities (Fig. 1.1a). Local populations loose lots of emigrants but gain only few immigrants. Therefore, dispersal

mortality has two effects on local dynamics: First, it stabilizes local population fluctuations by damping population peaks at over-compensation (Fig. 1.1b, called here fluctuation stabilizing effect, Gonzalez-Andujar and Perry 1993; Ruxton 1993; Ruxton et al. 1997; Amarasekare 1998). Secondly, it decreases the connectivity between local patches (called here connectivity reducing effect, Tischendorf and Fahrig 2000a; Münkemüller and Johst 2006). Consequently, increasing dispersal mortality does not alter the functional form of the bimodal relationship between spatial synchrony and the mode of local density regulation but shifts the maxima slightly towards over-compensatory density regulation and reduces their absolute values (Fig. 1.1d).

Density dependent dispersal and landscape dynamics have effects comparable to dispersal mortality (Fig. 1.2 and Fig. 1.3). Density dependent dispersal shows a connectivity reducing and fluctuation stabilizing effect (Fig. 1.3). The fraction of emigrants leaving very dense populations is much higher than that leaving sparsely populated patches (stabilizing effect), and the resulting pattern of dispersers is more heterogeneous (Münkemüller and Johst 2006). Frequent patch destruction in dynamic landscapes reduces synchrony by randomly interrupting the pattern of intrinsic population growth (Fig. 2.2, cf. Johst et al. 1999).

In sum, the analysed dispersal and landscape properties do not alter the general bimodal relation between spatial synchrony and the mode of local density regulation but shift it slightly towards stronger over-compensation and towards a lower overall level of synchrony. Supplementary results showed that although the selected reproduction model and the parameterisation influence the particular location of the bimodal curve, the bimodal shape is a general feature.

### *Metapopulation persistence*

Even in the same landscape and with the same dispersal ability, metapopulation persistence can differ considerably, depending on the mode of local density regulation. For both under-compensatory and strong over-compensatory density regulation, variability of local population sizes (Fig. 1.1b) and resulting local extinction risk (Fig. 1.1c) are high. In the former case this is due to low mean local population sizes (Fig. 1.1a) caused by a combination of demographic as well as environmental stochasticity and small growth rates. In the latter case it is due to intrinsic population crashes (Allen et al. 1993; Costantino et al. 1997; Ripa and Lundberg 2000). Even moderate synchrony makes these high local extinction risks dangerous for metapopulation persistence. Consequently, there is a unimodal relationship between persistence and the mode of density regulation with low persistence at both under-

compensation and strong over-compensation and high persistence in-between. However, it should be noted that the range of high metapopulation persistence comprises levels not only of low but also of high spatial synchrony (Fig. 1.1d and e).

Increasing dispersal mortality, density dependence of dispersal and landscape dynamics do not alter the general unimodal relation between metapopulation persistence and the mode of density regulation but shift the curve towards higher over-compensation (Figs. 1.2, 1.3). Consequently, persistence generally decreases for under-compensation and increases for over-compensation. This can be explained again by the two effects mentioned above. Species with under-compensation particularly suffer from the connectivity decreasing effect of dispersal mortality, density dependent dispersal and landscape dynamics. Their low local population sizes (Fig. 1.1a) depend on immigrants to support both still existing populations (rescue effect; decreasing extinction risk due to immigrants) and the recolonization of extinct patches (Fig. 1.1b). Species with over-compensation particularly benefit from the stabilizing and desynchronising effect of dispersal mortality, density dependent dispersal and landscape dynamics.

### *Synthesis and application*

Synthesizing and expanding earlier studies, we find a bimodal relationship between spatial synchrony and density regulation which causes a unimodal relationship between metapopulation persistence and density regulation. The general shapes of both relationships hold for different measures of synchrony, different dispersal and landscape properties and different population growth models and parameters. It is important to note that not only spatial synchrony alone but the combination of synchrony and local extinction risk determine metapopulation persistence. Species with over-compensating density regulation but still low local extinction risk can persist despite high synchrony. This is important when evaluating the effect which a certain level of spatial synchrony may have on metapopulation persistence.

Our results suggest different vulnerabilities of species with synchronous local population dynamics in landscapes with changing connectivity. These risks depend on their type of intraspecific local density regulation, i.e. whether they show (1) under-compensation or (2) over-compensation. (1) Metapopulations with under-compensation exhibit low local population sizes (Fig. 1.1a) and slow population growth. Therefore, they profit from immigrants counteracting the high local extinction risk (Fig. 1.1c) even if spatial synchrony is thereby increased (Fig. 1.1d; cf. section 'Metapopulation persistence'). Consequently, increasing landscape connectivity (e.g. reducing dispersal mortality through dispersal

corridors or reducing landscape dynamics, Figs. 1.1e, 1.2b) is an appropriate management strategy for these species.

Finding direct empirical evidence for the mode of density regulation is difficult since the elimination of all influencing factors is nearly impossible in the field. However, low local population densities, insufficient recovery, and a common trend towards extinction among subpopulations despite sufficient resources proved typical for under-compensation in our simulations and may therefore be indirect hints for under-compensation. Some endangered species in fragmented landscapes show a slow recovery from low population densities, despite a sufficient high carrying capacity of the landscape, which is very similar to that of species with under-compensation. For example, the need for helpers for reproduction (e.g. Florida Scrub-Jay, *Aphelocoma coerulescens*, or red-cockaded woodpecker, *Picoides borealis*) or long adult life spans with few young can cause slow population growth. For such species management plans that aim to increase landscape connectivity (Schiegg et al. 2002, Breininger et al. 1999) are appropriate. (2) Metapopulations with strong over-compensation exhibit deterministic population crashes. Therefore, it is more important to desynchronize their local dynamics than to counteract local extinction by immigrants (Fig. 1.1d). Consequently, decreasing landscape connectivity would be profitable for them (e.g. through increasing landscape dynamics or a more hostile matrix with high dispersal mortality). An empirical example for an endangered species which profits rather than suffers from decreasing connectivity is the flightless weevil, *Hadramphus spinnipennis*. Due to overexploitation of its local resources (patchily distributed plant species *Aciphylla dieffenbachia)* local population dynamics are characterised by deterministic extinction events. An appropriate conservation management for this species maintains or even enhances the hostility of the dispersal matrix to desynchronise these local extinction event (Schöps 2002, Johst and Schöps 2003).

Thus, our results emphasize to consider knowledge about density regulation in the evaluation of spatial synchrony and resulting conservation management of endangered species.

# 1.5 Appendix

Simulations start with the initialization of 10 patches, corresponding subpopulation sizes and the random arrangement of the spatial structure of the metapopulation (Fig. 1.6).

Afterwards, 100 time steps are computed each with the processes patch dynamics, subpopulation dynamics and dispersal. In the following, these steps are described in more detail:

*Initialisation.* For each of the 10 patches a maximum carrying capacity, $K_{i,max}$, is drawn from a uniform distribution ranging from 50 to 150 individuals, the current carrying capacity, $K_i(t=ini)$, is set equal to $K_{i,max}$. Initial population size for each patch, $N_{ini}$, is drawn from a uniform distribution ranging from 10 to $K_{i,max}$ individuals. Parameters for patch destruction (probability *fpd*), subpopulation growth (basic reproduction rate $R_{base}$, density dependence parameter *b*) and dispersal (mean dispersal distance $D_d$, dispersal mortality *m*) are set (Tab. 1.1).

*Spatial pattern.* Within a grid of 20*20 cells 10 cells are randomly chosen to host the 10 patches. The Euclidian distance between the patches is used as a distance measurement, $D_{ij}$. Based on $D_{ij}$, $D_d$ and the survival probability during dispersal $P_s$ (assumed to be linearly dependent on distance: $P_s = 1 - m * D_{ij}$) a transfer probability $P_{ij}$ is computed (cf. model section: equation 1.4).

*Patch dynamics.* Firstly, patches are able to regenerate after patch destruction. If the actual patch size $K_i(t)$, is smaller than maximum possible patch size $K_{i,max}$, $K_i(t)$ increases (cf. model section: equation 1.1). Secondly, patch destruction occurs with a probability *fpd*. If patch destruction occurs $K_i(t)$ is set to 1 and the current population size $N_i(t)$ is set to 0. The actual patch size $K_i(t)$ directly influences subpopulation growth in the considered step. Thus, patch dynamics are implemented explicitly into the population dynamics.

*Subpopulation dynamics.* Firstly, all subpopulations with $N_i(t)<2$ go extinct. Their population sizes are set to 0. All alive subpopulations grow with a temporally fluctuating reproduction rate $R_i(t)$ drawn from a uniform distribution ranging from 0 to $0.8*R_{base}$. Based on $N_i(t)$, $R_i(t)$, $R_{base}$, $K_i(t)$ and including a certain type of intraspecific competition given by the parameter *b* the expected population size after reproduction is calculated (cf. model section: equation 1.2). To include demographic stochasticity the actual population size is then drawn from a Poisson distribution using this expected population size as a mean.

*Dispersal.* Firstly, the number of emigrants per patch $N_{i,emi}(t)$ is drawn from a binomial distribution with the parameters $P_{e,i}(t)$ or $P_e$ respectively and $N_i(t)$. Secondly, based on the matrix of transfer probabilities (including the probability to die) and the number of emigrants, the number of immigrants for each patch $N_{i,immi}(t)$ is drawn from a multinomial distribution.

**Table 1.1:** Overview of variables (changing each time step), input parameters (varied systematically for different scenarios), input constants (not varied in the different scenarios, some of them are drawn from given distributions in the simulation runs for a particular scenario) and output variables. The subscript $i$ refers to a specific patch and $t$ to a specific time step.

| Symbol | Description | Process | Values | Type |
|---|---|---|---|---|
| **_State and derived variables_** | | | | |
| $N_i(t)$ | Population size | (Subpopulation dynamics) | | integer |
| $R_i(t)$ | Random reproduction rate | (Subpopulation dynamics) | $[0;0.8*Rbase]$ | double |
| $K_i(t)$ | Carrying capacity | (Patch dynamics) | $[0;K_{i,max}]$ | integer |
| $P_{e,i}(t)$ | Density dependent emigration rate | (Dispersal) | $[0.65;0.75]$ | double |
| $D_{ij}$ | Euclidian distance between patches | (Spatial pattern) | | |
| **_Input -parameters_** | | | | |
| $b$ | Density dependence parameter | (Subpopulation dynamics) | $e^{-2}$-$e^{2.7}$, step length 0.1 | double |
| $fpd$ | Patch destruction probability | (Patch dynamics) | 0, 0.5, 0.1, 0.15, or 0.2 | double |
| $m$ | Dispersal mortality | (Dispersal) | 0, 0.02, 0.04, 0.06, 0.08 or 0.1 | double |
| $v$ | Determines emigration rate | (Dispersal) | $0$-$3*10^8$ | double |
| $w$ | Density dependence of emigration | (Dispersal) | 0, 1, 3, or 5 | double |
| **_Input -constants_** | | | | |
| $N_{patches}$ | Number of patches | | 10 | |
| $N_{ini}$ | Initial population size | (Subpopulation dynamics) | $[10; K_{i,max}]$ | integer |
| $R_{base}$ | Basic reproduction rate | (Subpopulation dynamics) | 15 | double |
| $K_{i,max}$ | Maximum carrying capacity | (Patch dynamics) | $[50;150]$ | integer |
| $D_d$ | Mean dispersal distance | (Dispersal) | 1/10.32 | double |
| $P_e$ | Density independent emigration rate | (Dispersal) | $[0.65;0.75]$ | double |
| **_Output variables_** | | | | |
| | Metapopulation persistence: Percentage of simulations in which metapopulations survived 100 time steps | | | |
| | Mean subpopulation size over 100 time steps and 100 simulations | | | |
| | Mean variability of local populations over 100 time steps and 100 simulations | | | |
| | Mean number of local extinction events per 100 time steps and 100 simulations | | | |
| | Synchronization (if not mentioned otherwise: mean cross correlation based on Pearson $\Delta N$) | | | |
| $N_i(t)$ | Population size versus time | | | |
| Pearson $\Delta N$ | Pearson correlation coefficient of differences in local population sizes | | | |
| Kendall's $\tau$ | Modified version of Kendall's $\tau$ | | | |
| Pearson $N$ | Pearson correlation of local population size | | | |

Finally, the population size of the following time step, is re-calculated: $N_i(t+1) = N_i(t) - N_{i,emi}(t) + N_{i,immi}(t)$. To compare density independent and density dependent dispersal strategies on the basis of the same mean emigration probability we developed the following approach. First, we select a range of 0.65 to 0.75 in which the density independent emigration probabilities $P_e$ can vary and calculate the corresponding

output averaged over 100 simulations. Second, we systematically vary density dependent emigration $P_{e,i}(t)$ by varying $v$ and $w$ (cf. model section: equation 1.3; cf. Tab. 1.1 for parameter ranges of $v$ and $w$). For all combinations of $v$ and $w$ the expected emigration probability of each patch $P_{e,i}$ is determined. Finally, we include only those runs in the analysis in which the resulting mean emigration probabilities over 100 years and all 10 local populations are between 0.65 and 0.75. This ensures the comparison of density independent and density dependent dispersal on the basis of the same mean emigration probability with highly variable emigration probabilities in space and time at density dependent dispersal.
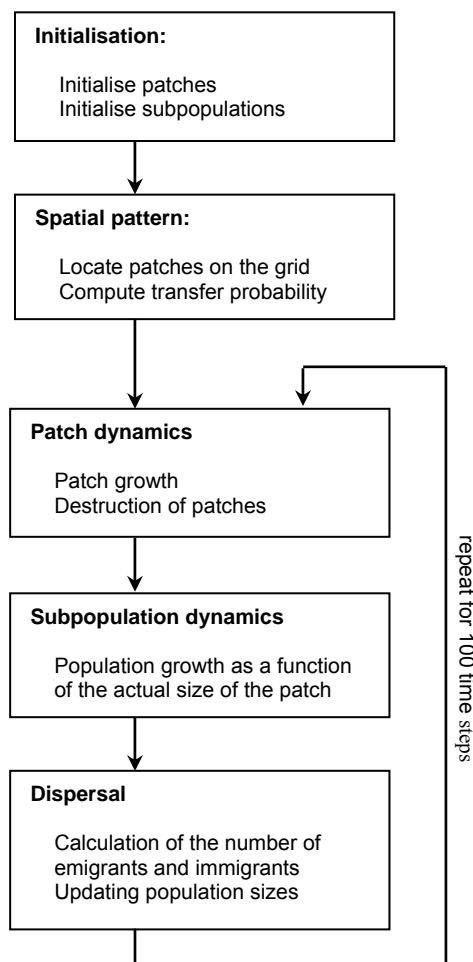


**Figure 1.6:** Flowchart of the simulation model

*Parameter space and outcome quantities.* We performed a sensitivity analysis to check to which parameters the outcome is sensitive. As we concentrate in this paper on the relationship

between synchronisation and the type of intraspecific competition, we show typical results for different scenarios of density dependent dispersal, dispersal mortality and landscape dynamics as these processes proved important for this relationship. Moreover, we tested different synchronisation measures and compared their performance.

# 2 Spatial synchrony through density independent versus density dependent dispersal [2]

Many theoretical studies support the notion that strong dispersal fosters spatial synchrony. Nonetheless, the effect of conditional versus unconditional dispersal has remained a matter of controversy. We scrutinise recent findings on a desynchronising effect of negative density dependent dispersal based on spatially explicit simulation models. Keeping net emigration rates equivalent, we compared density independent and density dependent dispersal for different types of intraspecific density regulation ranging from under-compensation to over-compensation. In general, density independent dispersal possessed a slightly higher synchronising potential but this effect was very small and sensitive compared to the influence of the type of local density regulation. Notable, consistent outcomes for the comparison of conditional dispersal strategies strongly relied on the control of equivalent emigration rates. We conclude that the strength of dispersal is more important for spatial synchrony than its density dependence. Most important is the mode of intraspecific density regulation.

## 2.1 Introduction

Dispersing individuals among patches have both positive and negative impacts on the dynamics and persistence of spatially structured populations or metapopulations. On the one hand, they can colonise extinct patches and thus support metapopulation persistence. On the other hand, they can synchronise local dynamics and subsequent local extinction events (spatial synchrony), and thus reduce the heterogeneous spreading of extinction risk (DenBoer 1968; Heino et al. 1997; Petchey et al. 1997; Matter 2001; Murrell et al. 2002; Johst and Drechsler 2003). Therefore, the synchronising potential of dispersal is a topic of continuing debate. Five main factors are identified in literature to affect the synchronising potential of dispersal: (1) the species ability to reach other patches determined by dispersal rate and/or

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[2] A paper with equivalent content is published in *Journal of Biological Dynamics* (Münkemüller and Johst 2007).

distance including dispersal mortality (Murrell et al. 2002; Johst and Drechsler 2003; Ruxton 1994; Ranta et al. 1995; Ripa and Lundberg 2000; Ashwin 2003), (2) the strength and spatial correlation of environmental fluctuations and landscape dynamics (Heino et al. 1997; Petchey et al. 1997; Matter 2001; Kendall et al. 2000; Johst and Drechsler 2003), (3) the type of local dynamics (Petchey et al. 1997; Matter 2001; Ripa and Lundberg 2000; Palmqvist and Lundberg 1998; Bjørnstad 2000), (4) species interactions (Liebhold et al. 2004; Koelle and Vandermeer 2005) and (5) the density dependence of dispersal (Ruxton and Rohani 1998; Ims and Andreassen 2005).

High emigration rates, large dispersal distances and a low mortality during dispersal are able to synchronise local dynamics over large spatial scales (Murrell et al. 2002; Münkemüller and Johst 2006). Environmental stochasticity can influence this process by amplifying or weakening the resulting synchronisation depending on the spatial scale and auto-correlation of the environmental influences themselves (Moran effect, Matter 2001; Ranta et al. 1998; Lande et al. 1999; Koenig 2002). However, the strength of the resulting spatial synchrony further depends on the type of local dynamics in the patches (Ripa 2000; Liebhold et al. 2004; Münkemüller and Johst 2006). Due to intraspecific competition, the per capita growth rate of a population is density dependent, and how this density dependence operates – in an under-compensatory, compensatory, or over-compensatory manner – may result in either equilibrium, cyclic or even chaotic dynamics (May 1974; Hassell 1975). It is known that synchronisation by dispersal is much stronger for over-compensatory than for compensatory density regulation (Murrell et al. 2002; Ripa and Lundberg 2000; Ripa 2000; Bjørnstad 2000; Münkemüller and Johst 2006; Liebhold et al. 2006). Additionally to intraspecific competition, interspecific interactions can influence the synchronising potential of dispersal (Liebhold et al. 2004; Koelle and Vandermeer 2005).

Recently, Ims and Andreassen (2005) stressed another important factor influencing the synchronising potential of dispersal: the density dependence of the emigration rate. The decision to leave the habitat and to disperse to another one can be conditional on the density in the patch. Ims and Andreassen (2005) studied Tundra voles, *Microtus oeconomus*. Even though this species is particularly well known for its spatially synchronised population dynamics (Ranta et al. 1997; Ims and Andreassen 2000; Andreassen and Ims 2001), dispersal movement did not act to synchronise subpopulation dynamics in the experimental part of their study (Ims and Andreassen 2005). The authors argued that this could be due to the observed negative density dependence of dispersal (emigration rate decreases with increasing density). In addition, they simulated population dynamics with a stochastic difference equation model

and parameters derived from their experimental study and again did not find a significant synchronising effect of negative density dependent dispersal. Assuming density independent dispersal (constant emigration rates) instead they could show a slight synchronising effect.

In sum, knowledge already exists about the effects of local dynamics, interspecific population interactions, and correlated environmental stochasticity on population synchrony. The role of dispersal in synchrony is well documented with regard to emigration rates, dispersal distances and dispersal mortality. However, studies on conditional dispersal are rare although strategies, such as density dependent dispersal, are fairly common (Ims and Andreassen 2005). In this study we provide a comparison of density independent and negative density dependent dispersal based on the control of equivalent emigration rates. We apply this comparison on both a study of Tundra voles by Ims and Andreassen (2005) and a more general population growth model. We argue that the situation is more complex than proposed by Ims and Andreassen and demonstrate that their results depend on the assumption that Tundra voles do not show intrinsic density fluctuations (cycles or chaos, in nature densities of Tundra voles often cycle, Ranta et al. 1998; Oksanen et al. 1999).

## 2.2 Model description

We studied two different spatial arrangements: a basic model that was very similar to the simple difference equation model of Ims and Andreassen (2005) and an extended model with higher complexity (a modified version of the metapopulation model by Münkemüller & Johst, 2006).

### Basic model

The basic model focussed on a two patch system. If not stated otherwise we followed Ims and Andreassen (2005) and described local population dynamics within a patch by a Gompertz type model:

$$N_{t+1,i} = N_{t,i} \cdot \exp\!\left(a - c \cdot \left(\ln\!\left(N_{t,i}\right)\right)^b\right) + \varepsilon_{t,i} \tag{2.1}$$

$N_{t,i}$ is the population density (continuous numbers) at time $t$ and $\varepsilon_{t,i}$ describes normally distributed, additive local white noise with mean zero and standard deviation 0.75. A minimum population density was assumed of $N_{t,\,i} = 1.0$ for reproduction (otherwise $N_{t+1,i}$ was

set to zero). The parameters $a = 0.43$, $b = 1$ and $c = 0.3$ have been estimated from experimental data by Ims and Andreassen (2005) and resulted in a mean population size at equilibrium $K_i = 4.2$ (carrying capacity). We considered different types of intraspecific competition ranging from under-compensatory, small *ln(b)*, up to over-compensatory density-regulation, large *ln(b)*. For *ln(b)* equal 0 density-regulation is compensatory. To keep the carrying capacity constant over all values of *b*, we have chosen parameter *c* in dependence on *b* according to the following formula:

$$c = 0.43 / \left( \ln\left(K_i\right) \right)^b$$

If stated so we additionally considered a Ricker type model to describe population growth:

$$N_{t+1,i} = N_{t,i} \cdot \exp\left(a - a \cdot \left(N_{t,i}/K_i\right)^b\right) + \varepsilon_{t,i} \qquad (2.2)$$

We accounted for two types of dispersal: density independent and negative density dependent dispersal. Negative density dependent emigration rates $\varphi_{t,i}$ were described by the logistic function used by Ims and Andreassen (2005):

$$\varphi\left(N_{t,i}\right) = \exp\left(-1.09 - 0.08 N_{t,i}\right) / \left(1 + \exp\left(-1.09 - 0.08 N_{t,i}\right)\right) \qquad (2.3)$$

Density independent dispersal was modelled via constant emigration rates. Under negative density dependent dispersal emigration rates decrease with increasing individual numbers. For the comparison of density independent and negative density dependent dispersal, the constant rates of density independent dispersal were set to the mean net emigration rates under negative density dependent dispersal. Thus, both dispersal types have the same mean magnitude of net emigration rate for each parameter combination (mean emigration rates ranged between 0.19-0.20). Comparable to Ims and Andreassen (2005), there was no mortality during dispersal.

### *Extended model*

The extended model focussed on a two or ten patch system with more complexity than the basic model including explicit spatial structure, heterogeneity in the carrying capacities and demographic stochasticity in the reproduction and dispersal process. Spatial structure was

included by a grid of 20 * 20 cells with randomly distributed habitat patches. The carrying capacity of each patch was drawn at random from a uniform distribution within a range of [1/2 $K_i$ , 3/2 $K_i$ ], with $K_i$ = 40. A higher carrying capacity was necessary because local population sizes were described via integer numbers.

The dynamics of the expected values of local population sizes followed equation (2.1) and (2.2), respectively. To include demographic stochasticity, the actual subpopulation sizes were drawn from a Poisson distribution with mean $N_{t+1,i}$. A minimum population size was assumed of two individuals for reproduction (otherwise $N_{t+1,i}$ was set to 0).

We accounted for the same types of dispersal as in the basic model. As higher mean carrying capacities have been assumed in the extended model, we had to modify equation (2.3) to obtain the same emigration rates as in the basic model when subpopulation size and local carrying capacity match:

$$\varphi(N_{t,i}) = \exp\left(-1.09 - 0.08 \cdot 4.2 \cdot \frac{N_{t,i}}{K_i}\right) \Big/ \left(1 + \exp\left(-1.09 - 0.08 \cdot 4.2 \cdot \frac{N_{t,i}}{K_i}\right)\right) \qquad (2.4)$$

We also analysed scenarios with stronger negative density dependence of dispersal

$$\varphi_{strong}(N_{t,i}) = \varphi(N_{t,i}) \cdot \left(2.5 - \frac{N_{t,i}}{K_i}\right)$$

and higher emigration rates compared to equation (2.4):

$$\varphi_{high}(N_{t,i}) = \varphi(N_{t,i}) \cdot 5$$

Dispersal was distance dependent with an exponentially decreasing probability $P_{ij}$ of an individual dispersing from patch $i$ to $j \neq i$ over the Euclidean distance $D_{ij}$ between the two patches (no effect for only two subpopulations):

$$P_{ij} = \exp\left(-\frac{1}{D_d} D_{ij}\right) \Big/ \sum_j \exp\left(-\frac{1}{D_d} D_{ij}\right) ,$$

where $D_d$ is the (species-specific) mean dispersal distance which was assumed to be 10 cells. To include demographic stochasticity in the dispersal process, the number of emigrants per patch $i$, $E_{t,i}$, was binomial distributed with $N_{t,i}$ trials and a probability of $\varphi_{t,i}(N_{t,i})$. The actual number of immigrants from patch $i$ was multinomial distributed with parameters $E_{t,i}$ and $P_{ij}$. There was no dispersal mortality included.

***Simulation experiments***

Simulation runs started with the random distribution of patches over the grid. In each time-step, density dependent local population dynamics were followed by dispersal. Spatial synchrony was determined by a mean cross-correlation coefficient (1000 simulation runs for each parameter combination). The mean cross correlation was based upon a Kendall's $\tau$ type of correlation coefficient (Ims and Andreassen 2005; Buonaccorsi et al. 2001):

$$\tau = 2 \cdot \frac{n_{same}}{n_{total}} - 1 , \tag{2.5}$$

where $n_{same}$ is the number of points in time local populations move in the same direction and are both alive and $n_{total}$ is the number of points in time both local populations are alive. The fraction term in equation (2.5) equals the average fraction of time (over all patches) that pairs of series agree about the direction of changes (Buonaccorsi et al. 2001).

The models were implemented in C++, numerical routines from the GNU Scientific Library (Galassi et al. 2002) were used for the probability distributions, and graphics were generated in R 2.2.0 (R Development Core Team 2007).

## 2.3 Results

In general, the synchronising effect of dispersal showed the expected pattern: Spatial synchrony was low at under-compensatory to compensatory density regulation and increased with increasing over-compensatory density regulation (Fig. 2.1). For two subpopulations at very strong over-compensation, local extinction risk increased due to the highly variable local dynamics and synchrony decreased consistently.
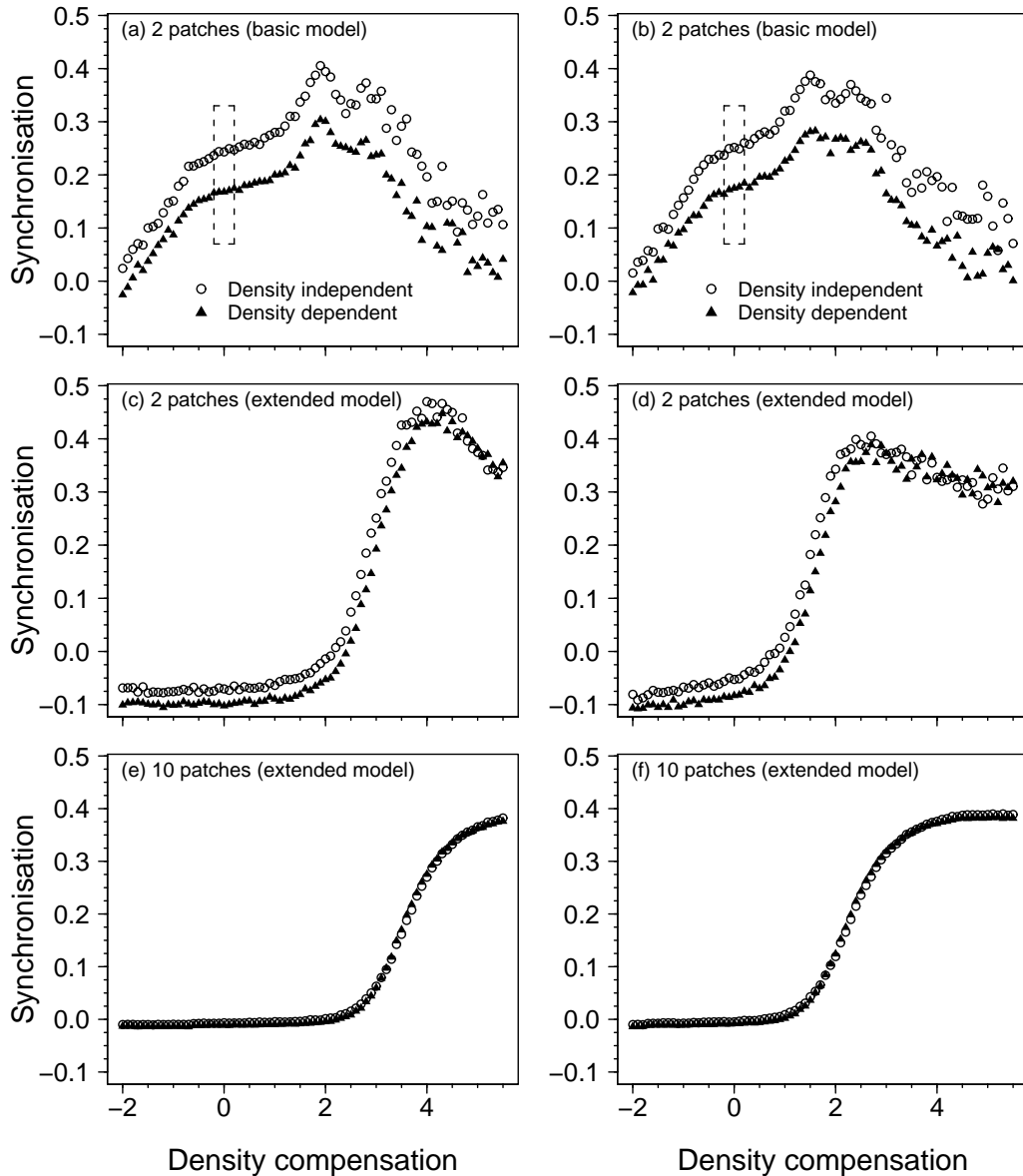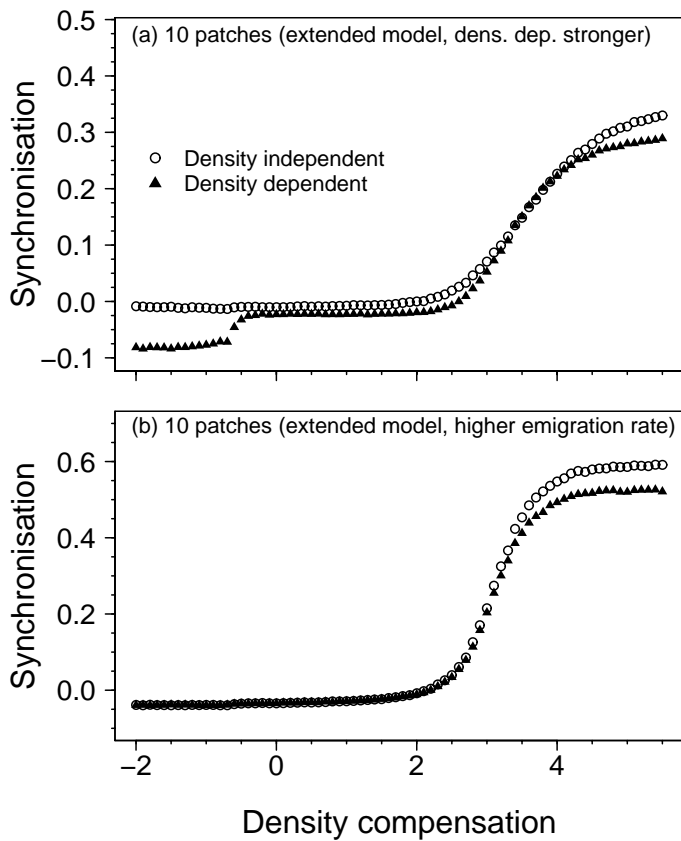
**Figure 2.1:** Synchronisation of local dynamics with density independent (circles) and negative density dependent (triangles) dispersal as a function of the strength of local density regulation (ln(b)) in spatially structured populations of two subpopulations in the basic model (a, b), two subpopulations in the extended model (c, d) and ten subpopulations in the extended model (e, f). In the first column Gompertz type dynamics (a, c, e) and in the second column Ricker type dynamics (b, d, f) govern population growth. The dissimilarity between the synchronising effects of density independent versus density dependent dispersal is much lower than the dissimilarity between compensatory and over-compensatory density regulation. The points within the dashed box show the equivalents to the values of Ims and Andreassen's model (Ims and Andreassen 2005).

This was not the case for ten subpopulations as local extinctions could still be compensated by colonisation events (Fig. 2.1a, b vs. c). Note that synchrony can also increase

at parameter combinations of very under-compensatory density regulation (Münkemüller and Johst 2006; Münkemüller and Johst 2007).

Results of the basic model showed that density independent dispersal is more effective than negative density dependent dispersal in synchronising local population dynamics (synchrony at compensating density regulation is 0.17 for density dependent and 0.24 for density independent dispersal, Fig. 2.1a, b dashed box). However, both types of dispersal allowed for effective synchrony at moderate over-compensatory density regulation. The type of local density regulation had a much stronger influence on synchrony than the type of dispersal (Fig. 2.1a, b).



**Figure 2.2:** Synchronisation of local dynamics with density independent (circles) and negative density dependent (triangles) dispersal as a function of the strength of local density regulation (*ln(b)*) in spatially structured populations of ten subpopulations in the extended model with stronger negative density dependence of dispersal (a) and higher emigration rates (b).

Two subpopulations in the extended model had lower differences in spatial synchrony between density independent and negative density dependent dispersal than in the basic model

(Fig. 2.1a, b vs. 2.1c, d) but higher than ten subpopulations in the extended model (Fig. 2.1e, f). In the extended model with ten patches synchrony did not differ between negative density dependent dispersal and density independent dispersal (Fig. 2.1e, f).

The described functional responses did not depend on the type of model we used to describe population growth: In qualitative outcome, the Gompertz type model and the Ricker type model are about equal (the same was true for Maynard Smith type dynamics; not shown results). Increasing the strength of density dependence of dispersal resulted in slightly higher levels of spatial synchrony for density independent than for density dependent dispersal, especially for strong under- and overcompensation (Fig. 2.2a). Increasing the emigration rate from around 0.2 to 0.88 increased the general level of synchrony but increased only slightly the difference in synchrony between density independent and density dependent dispersal. Again, the influence of local density regulation on spatial synchrony was much stronger than the density dependence of dispersal or the size of emigration rates (Fig. 2.1c vs. 2.2a and b).

These results did not vary significantly between models with continuous and those with discrete individual numbers (not shown results).

## 2.4 Discussion

Metapopulation theory has long suggested that dispersal is one of the important synchrony-inducing factors. However, the synchronising power of dispersal is likely to be conditional on different factors, and has been recently proposed to vanish under negative density dependent dispersal (Ims and Andreassen 2005).

In this study we scrutinise the generalisability of this proposition. Using a comparable population model (the basic model with compensatory local density regulation, Ims and Andreassen 2005) we could confirm that negative density dependent dispersal is less able to spatially synchronise population dynamics than density independent dispersal (Fig. 2.1a, dashed box). Moreover, similar to Ims and Andreassen (2005) who found mean synchronisation rates with highly overlapping confidence-intervals for density independent ($0.27 \pm 0.13$) and negative density dependent dispersal ($0.14 \pm 0.15$; including zero synchronisation only for the latter one) this difference was relatively faint. Further, we were able to demonstrate that this difference is very sensitive and can readily disappear. Increasingly over-compensatory density regulation proved a much stronger influence on synchrony than the type of dispersal (Fig. 2.1a) or the fundamental type of model used to

describe population growth. This became even more evident in the extended model. Here both, the influence of stochasticity during the dispersal process (Fig. 2.1b) and the higher number and spatially explicit configuration of patches (Fig. 2.1c) diluted the differences between the two dispersal strategies. Even a strong increase in emigration rates (Fig. 2.2b) or in the strength of negative density dependence of dispersal (Fig. 2.2b) resulted in a comparably small (with respect to the effects of intraspecific density regulation) and restricted (to strong under- or overcompensatory density regulation) increase in the difference between the two dispersal strategies. Interestingly, all these factors (demographic stochasticity in dispersal process, complex spatial structure, strongly negative density dependent dispersal, high emigration rates) did not decrease the difference in spatial synchrony between different types of intraspecific density regulation. This result consolidates the well documented synchrony supporting effect of unstable population dynamics (Ripa 2000; Liebhold et al. 2006; Münkemüller and Johst 2007).

In our simulation scenarios with moderate emigration rates the type of local density regulation finally moulded the level of synchrony with significant differences between compensatory and over-compensatory density regulation. Increasing emigration rates increased the level of synchrony whereas the type of dispersal strategy (density independent versus negative density dependent dispersal) led to comparably small and easily dilutable differences in synchrony. In contrast, earlier findings have shown a strong but inconsistent influence of dispersal strategies on the level of synchrony (Ylikarjula et al. 2000; Ims and Andreassen 2005). However, in these scenarios dispersal strategies and emigration rates were not varied independently but were mingled. As emigration rates influence the general level of synchrony (Fig. 3.2b, cf. Kendall et al. 2000; Münkemüller and Johst 2006; Williams and Liebhold 2000), we kept net emigration rates equal while comparing different conditional dispersal strategies. In doing so, it was possible to get consistent outcomes for the comparison of density independent and density dependent dispersal strategies over different types of intraspecific density regulation and increasing model complexity.

Our results add a missing piece to the (in most other respects) well analysed phenomena of spatial synchrony: In contrast to earlier findings, the synchronising effect of negative density dependent dispersal demonstrated to be as strong as that of density independent dispersal. When differences occurred, the level of spatial synchrony was typically smaller under negative density dependent than under density independent dispersal. However, differences were very sensitive to the assumptions and decreased in scenarios with higher complexity and realism. We conclude that the overall strength of dispersal is more important

for spatial synchrony than its spatio-temporal heterogeneity through conditional dispersal strategies. Most important is the mode of intraspecific density regulation.

A task for future work could be to study other types of conditional dispersal strategies and landscape structures. Furthermore, it would be interesting to investigate other types of internal population fluctuations e.g. caused by species interactions (competitive or trophic interactions). When interspecific interactions lead to similar spatial population fluctuation patterns then results would be comparable but complex multi-species dynamics and dispersal strategies could lead to unexpected results.

# 3 Hutchinson revisited: How and where do complex population dynamics promote species coexistence? [3]

Ecologists have long been searching for mechanisms of species coexistence especially since Hutchinson's raised the 'paradox of the plankton'. A promising approach to solve this paradox and to explain the coexistence of many species with strong resource overlap is considering over-compensatory density regulation with its ability to generate endogenous population fluctuations.

Previous work has analyzed the role of over-compensation in coexistence based on analytical approaches. Using a spatially explicit time-discrete simulation model, we vary the density regulation types for two species across the whole range from under- to strong over-compensation and analyze coexistence for different degrees of resource overlap and temporal and spatial heterogeneity.

We show that two otherwise identical species that differ in their density regulation are able to coexist if at least one species exhibits over-compensation. The species can coexist even if their resource requirements overlap completely. Analyzing the time series of population dynamics reveals how this coexistence mechanism works. It is not the over-compensator's endogenous fluctuations per se that promote coexistence, but the differential responses of the two competitors to these fluctuations. The over-compensator generates the density fluctuations but is the inferior competitor at strong amplitudes of those fluctuations; the competitor therefore gets frequent and dampens the over-compensator's amplitudes, but becomes inferior under dampened fluctuations. These species interactions cause a dynamic alternation of community states.

We show that this dynamic mechanism works in both temporally constant and varying environments as well as in homogeneous and fragmented landscapes. Our results highlight the importance of applying more flexible density regulation models to explore species interactions than the classical Lotka-Volterra equations.

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# 3.1 Introduction

The search for mechanisms of species coexistence has a long tradition in ecology. Already Lotka (1925) and Volterra (1926) investigated this question with a theoretical competition model in the early 20th century and found that intraspecific competition must be greater than interspecific competition to facilitate coexistence of two species. Gause (1934) complemented this finding by experimental work on *Paramecium* species and concluded that two species competing for the same resources cannot stably coexist. Hutchinson answered by raising the 'paradox of the plankton' (Hutchinson 1961). He pointed to the apparent contradiction between the principle of 'competitive exclusion' (Gause 1934) and the existence of many highly diverse natural communities living on strongly limited numbers of resources. This contradiction brings up the question which mechanisms enable the number of coexisting species to exceed the number of available resources (Armstrong and McGehee 1976; Lundberg et al. 2000; Szabo and Meszena 2006).

Coexistence mechanisms can be classified into equalizing and stabilizing mechanisms (Chesson 2000b). Equalizing mechanisms build on minimizing differences in average fitness while stabilizing mechanisms rely on increased intra- compared to interspecific competition strength, which disproportionately reduces the average fitness of the more abundant species (Chesson 1994; Chesson 2000b). Among the stabilizing coexistence mechanisms, some depend on heterogeneous distributions of species in space (i.e. spatial storage effects, Shmida and Ellner 1984; Hanski and Woiwod 1993; Chesson 2000b; Durrett and Levin 1998; Neuhauser and Pacala 1999). Others depend on fluctuations of population densities in time and can foster coexistence via (1) temporal storage effects or (2) via different nonlinear responses to common fluctuating abiotic or biotic limiting factors (Chesson 1994; Chesson 2003), as explained briefly below.

Temporal storage effects are based on external variations of the environment causing species' density fluctuations, e.g. through seasonal variations in resource growth or strong and frequent disturbances (Smith 1981; Grover 1990; Anderies and Beisner 2000; Davis and Pelsor 2001; Abrams 2004; Kooi and Troost 2006).

Fluctuations of abiotic resources can emerge from different nonlinear consumer responses and lead to coexistence of many species on a handful of resources in continuous time models (Huisman and Weissing 1999; Huisman and Weissing 2002). At least three resources are needed, and there is an ongoing debate regarding the robustness of the effect, i.e. the size of

the parameter space under which this behaviour can be observed (Armstrong and McGehee 1976; Armstrong and McGehee 1980; Schippers et al. 2001; Huisman et al. 2001). In contrast, competition for biotic resources can lead to the coexistence of two or more consumers on a single resource (Armstrong and McGehee 1980; Zicarelli 1975; Abrams 2004; Ruxton 1996; Kaitala et al. 1999). In this case, coexistence requires at least two differences in species traits: first in the type of functional response in resource use and second in the minimum resource requirements.

In summary, models of species coexistence to date mostly consider factors that relate to fluctuations of external environmental factors or to species interactions with biotic resources. However, it is well known that fluctuations in population dynamics can also occur just through intrinsic growth dynamics of one species alone, such as over-compensatory density regulation (May 1975; May 1976; Johst et al. 2008). In this case, individuals scramble for coveted resources and populations over-compensate deviations from carrying capacities which results in frequent peaks and crashes in abundances (cyclic and chaotic dynamics). With compensatory density regulation, individuals follow strategies that effectively avoid resource over-use and population sizes fluctuate around carrying capacity only due to stochastic events (equilibrium dynamics). With under-compensatory density regulation, populations under-compensate deviations from carrying capacities and the adjustment of population sizes to carrying capacities is slow (delayed dynamics). For example, storage capacities may lead to a delayed response if resources decline.

Although over-compensatory and under-compensatory density regulation and the resulting dynamics have been investigated with respect to single species persistence (Ripa and Lundberg 2000; Murrell et al. 2002; Münkemüller and Johst 2006; Münkemüller and Johst 2007), only few studies have investigated their contribution to species coexistence. Damgaard (2004) expanded the Lotka-Volterra model of coexistence (Volterra 1926; Lotka 1925) to a situation where both species exhibited the same over-compensatory density regulation and showed that – in agreement with the classical Lotka-Volterra competition model – coexistence was dependent on stronger intraspecific than interspecific competition. Other authors found that differences in the types of density regulation can facilitate coexistence under certain assumptions of landscape configuration and interaction behaviour (Getz 1996; Johansson and Sumpter 2003; Edmunds et al. 2003; Kuang and Chesson 2008). Analytically analyzing coexistence conditions at the limit of periodic behaviour, Adler (1990) and Cushing (2007) provided evidence of oscillatory coexistence of two species with complete resource overlap, i.e. intraspecific competition equalling interspecific competition.

However, to date no study has systematically explored differences in the type of density regulation for a wide parameter range from under- to strong over-compensation. In particular, investigations beyond the cyclic range (including chaotic dynamics) and for different spatial and temporal landscape characteristics are missing. In this study, we evaluate when and how two species are enabled to coexist through over-compensatory density regulation even if resources completely overlap. To identify the underlying mechanism of this coexistence we analyze time series of community dynamics. We disentangle the relationship between intrinsically generated population fluctuations and trends in population growth indicating temporary superiority of the competitors. By doing so, we are able to reveal how species interactions create dynamic coexistence. By gradually decreasing the degree of resource overlap, we analyze the mechanism of coexistence through over-compensation for decreasing competition pressure and compare results with outcomes of the classical Lotka-Volterra competition model. Finally, our process-based modelling approach allows us to include temporal and spatial heterogeneity and thus to investigate the effects of disturbances and landscape fragmentation on the coexistence-promoting effect of over-compensation.

## 3.2 Model description

*Model*

We simulate a two-species community with time-discrete dynamics. The species can differ in their density regulation type, but all other attributes are identical. Resources of the species can overlap completely, only partly or not at all. We compare combinations of different 'landscape' situations: (a) fragmented vs. unfragmented landscapes (populations occupy four patches with inter-patch dispersal, or only a single patch) and (b) disturbed vs. undisturbed landscapes.

Time-discrete local population dynamics of species A and B are described by an extended version of the Maynard Smith and Slatkin equation (1973; see also Hassell and Comins 1976):

$$N_A(t+1) \sim Pois\left(\frac{N_A(t) \cdot R}{\left(1 + (R-1)\left((N_A(t) + aN_B(t))/K\right)^{b_A}\right)}\right)$$

$$N_B(t+1) \sim Pois\left(\frac{N_B(t) \cdot R}{\left(1 + (R-1)\left((N_B(t) + aN_A(t))/K\right)^{b_B}\right)}\right)$$

The population sizes of species *A* and *B* at time *t* are given by $N_A(t)$ and $N_B(t)$. Both species have the same maximum growth rate, *R*. It is set to 5 per time step, which seems reasonable for many species with low to medium body mass, e.g. for insects and small mammals (Sinclair 1989). Local species' carrying capacities *K* are set to 320 or 80 individuals (i.e., 320 individuals in the single patch landscape, 80 individuals per patch in the four patch landscape with small patches and 320 individuals per patch in the four patch landscape with large patches). The parameter *a* describes the resource overlap of the two species and thus the strength of interspecific relative to intraspecific competition. It is called competition coefficient. In most cases we keep inter- and intraspecific competition strength equal (competition coefficient *a* = 1). Exceptions are the analyses without interspecific competition (*a* = 0; Fig. 3.2) and the analyses that explore the effect of the competition coefficient on coexistence (systematic variation of *a;* Fig. 3.5).

Both species differ only in their type of density regulation, which is characterized by $b_A$ and $b_B$ (*b* < 1 corresponds to under-compensating, *b* = 1 to compensating, and *b* > 1 to over-compensating density regulation). In this way, a wide range of combinations of density regulation types from under-compensation to strong over-compensation can be studied at given growth rates, carrying capacities and competition coefficients. We account for demographic stochasticity by realizing random numbers from a Poisson distribution. We independently and randomly initialize populations for each species by drawing from a uniform distribution between *10* and *10+K* individuals.

In the fragmented landscape, dispersal occurs after local population growth. The population size after dispersal $N_i(t,d=1)$ is equal to the one prior to dispersal, $N_i(t,d=0)$, minus

the number of emigrants, $N_{emi,i}(t)$, and plus the number of immigrants. The number of emigrants per patch is drawn from a binomial distribution with $N_i(t,d=0)$ number of trials and emigration rate $p_{emi}$. The number of immigrants from patch $i$ to patch $j$ is drawn from a multinomial distribution with $N_{emi,i}(t)$ trials and transfer probability $p_{ij}$. The matrix of transfer probabilities, with entries $p_{ij}$, describes the probability to move from patch $i$ to patch $j$. Values decrease exponentially with the Euclidean distance between patches, $D_{ij}$, measured in units of grid cells:

$$p_{ij} = \frac{\exp\left(-\frac{1}{DD}D_{ij}\right)}{\sum_j \exp\left(-\frac{1}{DD}D_{ij}\right)} \cdot \exp\left(-mD_{ij}\right)$$

The mean distance over which both species are able to disperse is defined by $DD$, and the dispersal mortality rates are defined by $m$. The denominator scales the transfer probabilities $p_{ij}$ such that they add up to one over all $j$ in the absence of dispersal mortality (i.e. for the special case $m=0$). Emigration probability, dispersal distance and dispersal mortality rate $m$ are equal for both species.

Disturbances are introduced by an additional mortality rate and occur after population growth and dispersal. Disturbances randomly reduce local density by $D_s(t) \cdot N(t)$ individuals, where $D_s(t)$ ranges from 0 to 0.05 for each species and is independently drawn in each time step.

*Simulation experiments and output*

We varied density regulation from under-compensatory (minimum: $ln(b)=-2$) to strong over-compensatory density regulation (maximum: $ln(b)=2$) for both species (Tab. 3.1). For each combination of density regulation types (see Tab. 3.1), 100 simulations each with 1000 time steps were conducted, and from these we derived the survival probability of each species as well as the coexistence probability (proportion of simulations where both species survived 1000 time steps).

In the analysis of the time series of species' densities, we defined long-term growth trends by estimating locally weighted linear fits for population sizes as a function of time using a loess smoother (cf. function loess in R 2.2.0, R Development Core Team 2005). We measured

the amplitudes of the over-compensating species' density fluctuations via the absolute differences in the densities between consecutive time steps. Using again a loess smoother for a locally weighted fit, we then analyzed how the growth trends depend on amplitudes.

**Table 3.1:** Overview of (a) parameters that were varied across simulation experiments and (b) parameters that were kept constant across all simulation experiments (but some were drawn from given distributions).

| Symbol | Description | Values | Type |
|---|---|---|---|
| *(a) Parameters varied in simulation experiments* | | | |
| $PN$ | Patch number | 1 or 4 | integer |
| $K$ | Carrying capacity of patch $i$ | 80 or 320 | integer |
| $D_s(t)$ | Strength of disturbance for species $s$ at time $t$ | 0 or [0;0.05] | double |
| $b_s$ | Type of density regulation of species s | [exp(-2);exp(2)] | double |
| $a$ | Resource overlap | 0, 1 or [0; 1.2] | double |
| $p_{emi}$ | Emigration rate | no dispersal or 0.1 | double |
| $m$ | Dispersal mortality rate | no dispersal or 0.05 | double |
| $DD$ | Dispersal distance | no dispersal or 20 | double |
| *(b) Parameters kept constant across all simulation experiments* | | | |
| $N_{ini,s}$ | Initial population size of species $s$ | [10; 10+K] | integer |
| $R$ | Maximum growth rate | 5 | double |

To validate coexistence probabilities we additionally analyzed invasibility and monitored the probability to invade the population of the respective competitor with very few invaders. Both analyses gave comparable results, and thus we only report coexistence probabilities. We further repeated the experiments under the exclusion of stochasticity. We found no qualitative changes in the results and thus report only those including stochasticity.

The simulation model was implemented with the Borland C++ Builder 5 using numerical routines from the GNU Scientific Library (GSL Team 1992) for the probability distributions. Graphics and statistics were generated in R 2.2.0 (R Development Core Team 2005).

## 3.3 Results

We investigated coexistence of two species with complete resource overlap ($a$=1, conspecific individuals cause the same competitive pressure as heterospecific individuals) and analyzed the time series of population densities to understand their dynamic interactions. The simulations (Fig. 3.1) showed that competitive interactions of two identical compensators ($ln(b)$=0, $a$=1) result in the random extinction of one species (Fig. 3.1a). The same was true for two identical over-compensators. However, when a compensating ($ln(b)$=0) and an over-

compensating species (*ln(b)*=1.5) competed with each other, both species were able to coexist (Fig. 3.1b, c).
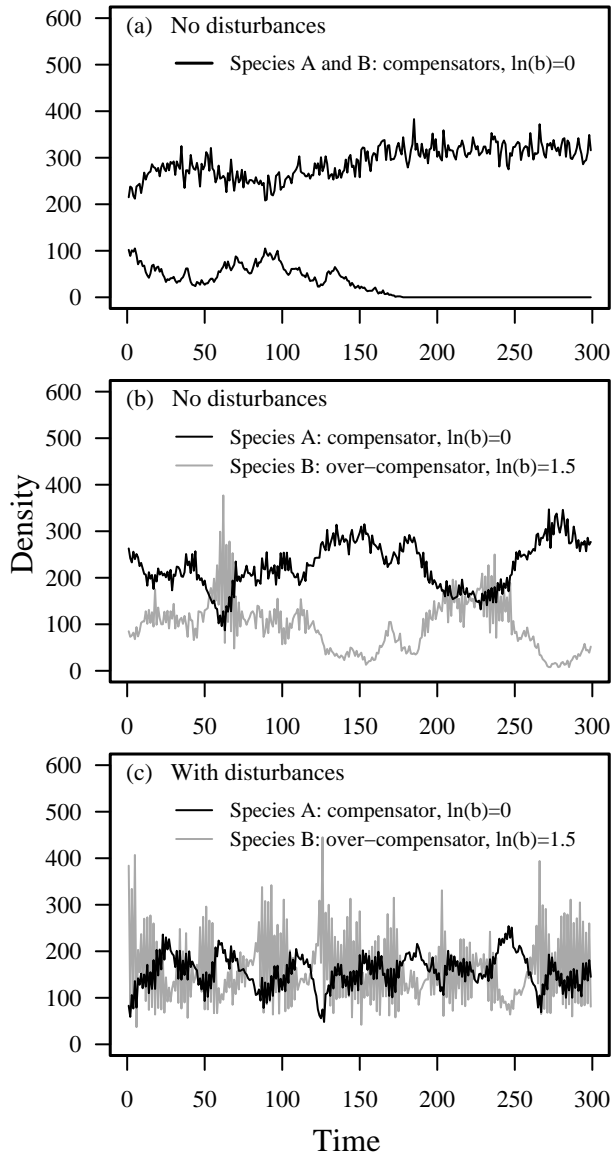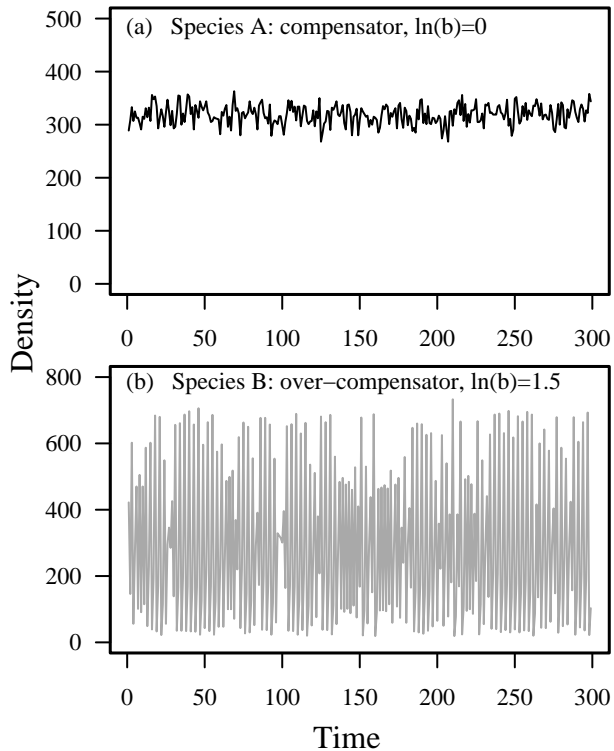


**Figure 3.1:** Population densities of two competing species over 300 time steps on one patch (for higher detail only the first 300 of 1000 time steps are shown): (a) equal types of density regulation without disturbances, (b) different types of density regulation without disturbances and (c) different types of density regulation with disturbances. Intraspecific competition is as strong as interspecific competition (*a*=1).

Interspecific interactions dampened the fluctuations of the over-compensator, i.e. amplitudes were much larger without interspecific interactions (*a*=0, Fig. 3.2a) than with

interactions ($a$=1, Fig. 3.1b, c). More specifically, amplitudes were buffered most strongly when the compensating species was more frequent than the over-compensating species.



**Figure 3.2:** Population densities of two non-interacting species over 300 time steps on one patch (for better detail only the first 300 of 1000 time steps are shown): (a) compensating density regulation and (b) over-compensating density regulation.

In contrast, amplitudes of the compensator were comparably strong without ($a$=0, Fig. 3.2b) and with interspecific interactions ($a$=1, Fig. 3.1). The local regression analysis between the over-compensators' amplitudes and species' growth trends revealed two alternating and mutually advantageous dynamic situations for the species (Fig. 3.3). Low to moderate amplitudes of the fluctuations resulted on average in a positive growth trend of the over-compensator but in a negative growth trend of the compensator, and vice versa. This was found to be a general pattern, but the absolute magnitude of the amplitude where the switch from positive to negative growth rates for the over-compensator and the competitor occurred (i.e., where both species displayed zero growth) varied between simulations. However, within each simulation the switch point of zero growth was identical for both the over-compensator and the competitor.
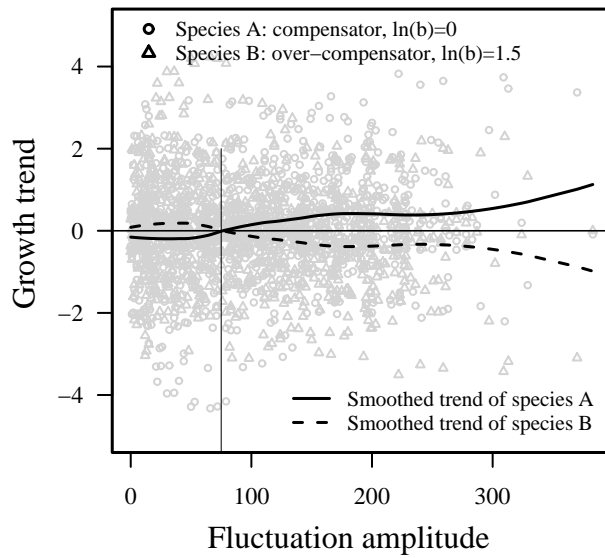
**Figure 3.3:** Long-term trends in population growth of both species depend on the over-compensator's fluctuation amplitudes. The figure provides an example for competing species on one patch with disturbances (cf. Fig. 3.1c, Fig. 3.4b). The vertical line marks the switch at which the growth trends of both species change their algebraic sign.

In a second step, we varied the combinations of density regulation types along a continuum from under-compensatory to strong over-compensatory density regulation to explore the robustness of this coexistence mechanism (Fig. 3.4). Generally, coexistence was possible if at least one species showed over-compensation and the other species differed in its density regulation type (Fig. 3.4, green areas). No coexistence occurred if both species had the same density regulation type (Fig. 3.4, cells along the diagonals). From under-compensation to moderate over-compensation, the species with stronger over-compensation was superior, i.e. species A outcompeted species B (Fig. 3.4, yellow areas), but from moderate to strong over-compensation the species with less over-compensation was superior, i.e. species B outcompeted species A (Fig. 3.4, blue areas). In the undisturbed and unfragmented landscape, the number of combinations of density regulation types leading to coexistence was small (Fig. 3.4a, small green area). However, light disturbances increased this number greatly and revealed a robust coexistence mechanism (Fig. 3.4b, large green areas).
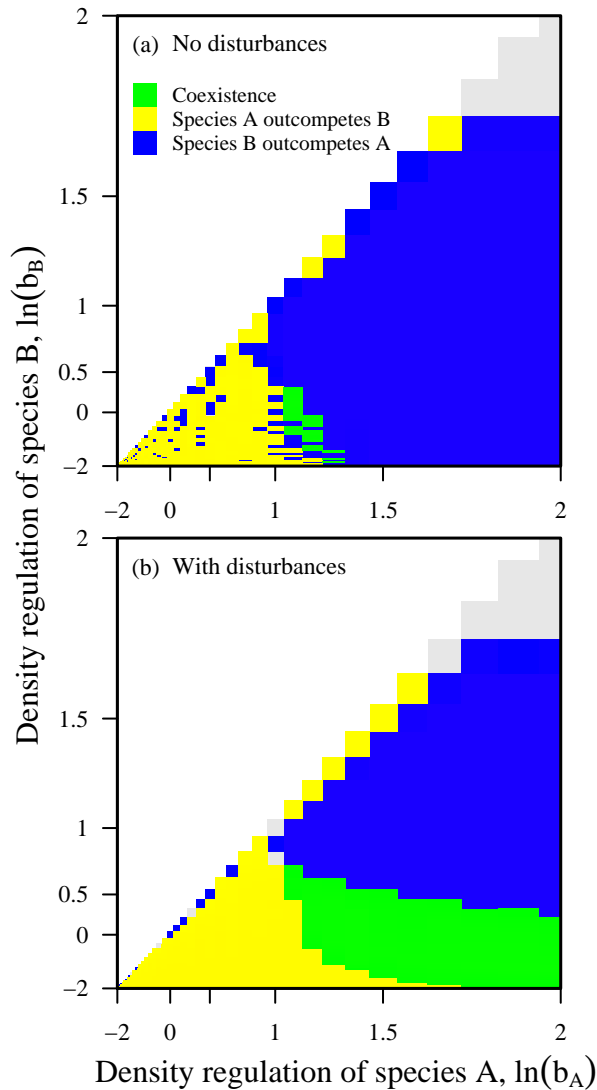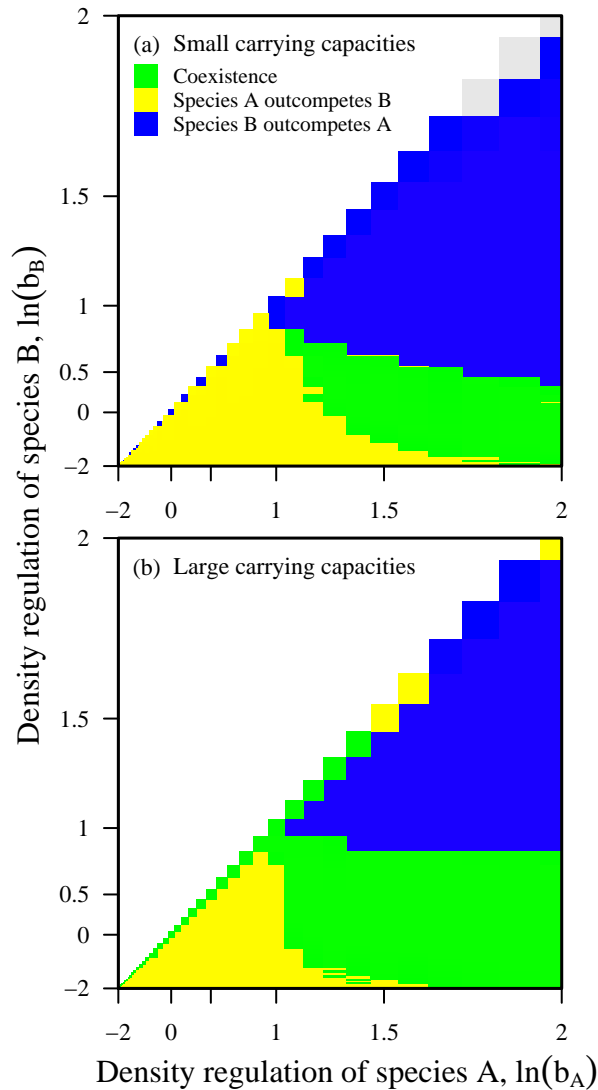
**Figure 3.4:** Coexistence probability of two species that differ only in their types of density regulation (ln(*b*)<0: under-compensation, ln(*b*)=0: compensation, ln(*b*)>0: over-compensation) over 1000 time steps. We analyzed different landscape situations on a single patch: (a) without disturbances, and (b) with disturbances. The colours code the competition outcome: green marks coexistence probability > 0.5, yellow marks coexistence probability <= 0.5 and persistence probability of species A > 0.8, and blue marks coexistence probability <= 0.5 and persistence probability of species B > 0.8. The presented output for $b_A >= b_B$ is equal to the output of $b_A <= b_B$ because species only differ in *b*.

In a third step, we studied coexistence in a spatially heterogeneous landscape. Fig. 3.5 shows that in a landscape with four patches a broad range of combinations of density regulation types allowed for coexistence. However, the size of the coexistence window critically depended on patch size (Fig. 3.5a, b). Coexistence probabilities increased with higher carrying capacities.

**Figure 3.5:** Coexistence probability of two species that differ only in their types of density regulation (ln($b$)<0: under-compensation, ln($b$)=0: compensation, ln($b$)>0: over-compensation) over 1000 time steps in a fragmented landscape. We analyzed different landscape situations without disturbances: (a) four small patches, and (b) four large patches. The colours code the competition outcome: green marks coexistence probability > 0.5, yellow marks coexistence probability <= 0.5 and persistence probability of species A > 0.8, and blue marks coexistence probability <= 0.5 and persistence probability of species B > 0.8. The presented output for $b_A >= b_B$ is equal to the output of $b_A <= b_B$ because species only differ in $b$.

In addition to the experiments where intraspecific was equal to interspecific competition strength ($a$=1) and those without interspecific interactions ($a$=0), we gradually increased the competition coefficient $a$ (Fig. 3.6). Species with equal density regulation types (equal $b$) were able to coexist only if interspecific competition was weaker than intraspecific

competition (*a*<1, Fig. 3.6a, left hand side of vertical line).
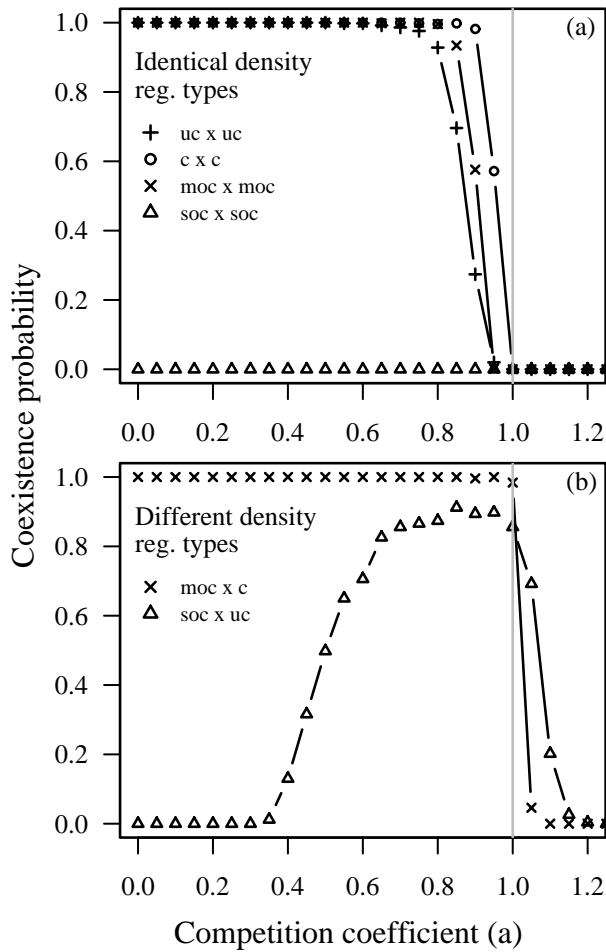


**Figure 3.6:** Coexistence probability of two species over 1000 time steps for different competition coefficients and different density regulation types (uc: under-compensation, ln(*b*)=-1, c: compensation; ln(*b*)=0, moc: moderate over-compensation, ln(*b*)=1.5, and soc: strong over-compensation, ln(*b*)=2). In (a) the competing species have equal types of density regulation and in (b) types of density regulation differ. The figures provide an example for competing species on one patch with disturbances (cf. Fig. 3.1c, Fig. 3.3b). The vertical lines mark the value of *a* where intraspecific equals interspecific competition strength.

How weak it had to be depended on the type of density regulation. However, if species differed in density regulation types and one species showed over-compensation, coexistence was possible even if interspecific was equal to or stronger than intraspecific competition (1<*a*<1.2, Fig. 3.6b, right hand side of vertical line). In particular, interspecific competition allowed a strong over-compensator that could not persist in isolation to coexist with another

species (Fig. 3.6b, extinction of a strong over-compensator at $a<0.35$, but survival and coexistence with an under-compensator at $0.35<a<1.2$). Hence, interspecific competition clearly broadened the survival range that results from the various density regulation types.

# 3.4 Discussion

Using a simple time-discrete population model we show that species that are identical in their growth rates, carrying capacities and intra- and interspecific competition strengths are able to coexist even with complete resource overlap if (1) they differ in their types of density regulation and (2) at least one species shows over-compensating density regulation. Two dynamically alternating and mutually advantageous biotic system states provide the underlying mechanism of coexistence through over-compensation. These states are internally generated, and the different fluctuation strength of the over-compensator's population density in these states is the key element. At low to moderate fluctuations, the over-compensator is the stronger competitor with a higher effective growth trend compared to the competitor (Johansson and Sumpter 2003). This leads to increasing dominance of the over-compensator's density in the population. However, high densities amplify the over-compensator's intrinsic fluctuations. At strong fluctuations, the competing species can use the emerging density depressions as temporal niches, provided that its density regulation is more compensatory. Consequently, the competing species has the higher effective net growth rate and increases its relative frequency in the population. However, the over-compensator's fluctuations are buffered at a high frequency of the competing species, and thus the over-compensator becomes the stronger competitor again. In sum, coexistence through over-compensation is possible because the over-compensator tends to generate fluctuations from which it suffers and the competing species tends to dampen these fluctuations from which it benefits (Figs. 3.1, 3.3). Thus, the essence of this mechanism is the interplay between different dynamic community states emerging from interacting species with different density regulation types (Fig. 3.3). Kuang and Chesson (2008) suggested a similar interplay between two alternating states for a plant community facing seed predation. In their model the relative nonlinearity of the growth functions was generated by life history trade-offs between seed productivity and persistence in the seed bank rather than through density regulation.

We show that coexistence through over-compensation occurs over a wide parameter range. It works especially well for large (sub)populations and best in slightly disturbed and/or

fragmented landscapes. As large population sizes serve to buffer density fluctuations and help to prevent extinction during density drops, our results suggest that communities depending on the mechanism of coexistence through over-compensation are likely to be sensitive to landscape fragmentation, in particular if remaining patches are small and poorly connected (Fig. 3.5). In slightly disturbed and/or fragmented landscapes, processes occur that (independently of density) remove individuals from the population. This lowers overall density and thus strengthens the impact of alternating positive growth rates leading to better coexistence (Fig. 3.3). Interestingly, competition between species could even promote coexistence when species survival without competition is not possible. In isolation, species with very strong over-compensation produce high density fluctuations that lead to long-term extinction. Only if these fluctuations are buffered, for example due to interspecific competition, species are able to persist (Fig 3.5b).

Within Chesson's classification scheme (Chesson 1994; Chesson 2000b) two broad categories of coexistence mechanisms that depend on fluctuations in population densities emerge: storage effects and relative nonlinearity. The mechanism we have investigated in detail here, coexistence through over-compensation, results from temporal fluctuations that are internally produced by the nonlinear responses of species population growth to competition. It thus can be associated with Chesson's category of relative nonlinearity. This is the case even though Chesson's approximations are analytical and thus only accurate if population fluctuations are small (Chesson, personal communication). However, coexistence through over-compensation differs from other examples in three important ways: (1) it can be described by a relatively simple and well-established population growth model (Maynard Smith and Slatkin 1973; Hassell and Comins 1976), the coexisting species differ in a single trait only (the type of competition for resources), and no trade-offs or storage effects are needed (in contrast to Kuang and Chesson 2008); (2) the limiting factor is the common density of both species in relation to the shared carrying capacity. It allows coexistence at complete resource overlap (in contrast to Armstrong and McGehee 1980; Schippers et al. 2001; Huisman et al. 2001); and (3) relative nonlinearity in the response to the limiting factor per ser is not sufficient for coexistence but one species has to show over-compensatory density regulation. In this case, the mechanism is robust over a wide parameter range and in a variety of landscapes (cf. comments on Huisman's work, Schippers et al. 2001). Nevertheless, it remains an interesting question how coexistence through over-compensation would work if more species and resources were involved.

What is the relevance of this novel but so far theoretical coexistence mechanism for real

ecosystems? The type of density regulation is a species trait that is particularly difficult to measure in field experiments (Godfray et al. 1990; Morris 1990). Estimates of local density regulation depend on time series over long time intervals and with a sufficient number of data points so that information on frequency, amplitudes and intervals of fluctuations can be captured. Such long time series are rarely available. Furthermore, processes such as environmental and demographic stochasticity, dispersal in fragmented landscapes, competition, predator-prey interactions in food webs or differential uptake rates of multiple and possibly fluctuating resources may 'dilute' the effects of density dependence and make it very difficult to decide which type of density dependence underlies observed fluctuations. Even for time series derived from simulation models, it is difficult to estimate the type of density regulation without an *a priori* knowledge of the processes included in the model. However, in spite of these difficulties to evaluate density regulation types in empirical systems, many researchers have suggested that it is likely that the different types of density regulation have a significant effect in ecosystem functioning (reviewed in Hastings *et al.* 1993). For example, several studies have provided evidence of chaos, as it could emerge under over-compensatory density regulation, in experimental as well as 'natural' conditions (Godfray et al. 1990; Hastings et al. 1993). Field studies suggest over-compensating density regulation as a possible mechanism in the competition for resources especially for species with density regulation in early life-stages (Sinclair 1989; e.g. for butterflies such as cinnabar moths *Tyria jacobaeae*, Vandermeijden *et al.* 1991, beetles such as southern pine beetle *Dendroctonus frontalis*, Reeve *et al.* 1998, and small mammals such as *Arvicola terrestris*, Aars *et al.* 2001, and *Microtus ochrogaster,* Getz *et al.* 2006). In sum, there is considerable evidence for a range of density regulation types in empirical systems. We suggest that particularly in communities with high species diversity but apparently limited resources species coexistence may rely critically on the differentiation in the types of density regulation as demonstrated in our theoretical investigations. Examples are the high small mammal and insect biodiversity in some parts of the tropical rainforest zone where many species with no apparent differentiation in physiological characteristics or resource requirements coexist, or the marine plankton communities that are highly diverse although only few resources are potentially limiting.

# 4 Disappearing refuges in time and space: How climate change and habitat isolation threaten species coexistence [4]

Understanding the potential impacts of climate change and patch isolation on communities represents a major challenge for ecology. To complement the advances made in typically single-species, climate niche modelling a new focus on multi-species systems utilising process-oriented approaches is required.

Here, we apply a two-species simulation model to analyse coexistence in landscapes with different degrees of climate change and isolation. The model explicitly considers dispersal between habitat patches, local competition and growth on a common resource. Species differ only in their density regulation. In this system two distinct mechanisms of coexistence emerge: (1) Stabilized coexistence of species that differentiate along a gradient of density regulation, ranging from under- to strong over-compensation, if at least one species displays over-compensation and (2) neutral coexistence of species with nearly identical traits. Stabilized coexistence dominates in well-connected landscapes with high habitat availability while neutral coexistence dominates in more fragmented and isolated landscapes.

Our model highlights that geographic range-shifting due to climate change, together with patch isolation, can severely impact coexistence. The strength of these impacts considerably differs depending on the underlying coexistence mechanism. Neutrally coexisting assemblages are particularly sensitive to strong habitat isolation, while stabilized coexistence is much more sensitive to climate change. Coexistence can be reduced even when the rate of environmental change leads to relatively low rates of range shifting implying that the structure of many communities may be threatened by the current episode of climate change.

Overall, our results highlight that a deeper understanding of the processes structuring communities is required if we are to better understand the potentially synergistic threats of

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climate change and patch isolation and ultimately develop management plans for specific communities.

## 4.1 Introduction

Landscape fragmentation and climate change have been identified to be among the most severe causes of global population decline and species extinction (Sala et al. 2000; Thomas et al. 2004). A substantial body of work has been devoted to understanding the potential impact of these environmental factors on species' ranges (e.g. Araujo and Rahbek 2006; Thuiller et al. 2006; Hatfield and LeBuhn 2007; Kruess and Tscharntke 1994). The great majority of this work utilises correlational approaches to relate current distributions to current climate and then projects future distributions onto future climate (Thuiller et al. 2004; Araujo et al. 2004). However, there is an increasing recognition that, on their own, these well-established methods are insufficient for predicting future patterns of biodiversity, and that a deeper ecological understanding of the process of range shifting is required (Guisan and Thuiller 2005; Heikkinen et al. 2006; Araujo and New 2007). Some progress has already been made on understanding how both the intrinsic population dynamics (Best et al. 2007) and the dispersal characteristics of a species (Higgins et al. 2003; Travis 2003; Midgley et al. 2006) determine its ability to track a changing climate, i.e. its ability to move from currently-suitable to future-suitable areas. So far, all these correlational models take a single-species approach. In reality, both the current distribution of a single species and its response to environmental change depend upon other species within the community. With the exception of a few rather specific examples (Ferrier and Guisan 2006; Brooker et al. 2007) there is a lack of formal modelling considering how the processes that structure a community under constant climatic conditions determine how the elements of that community will respond to climate change.

In this paper, we address these issues by analysing coexistence of two interacting species under the increasing pressure of patch isolation and climate change. We explicitly focus on whether and to what extent different coexistence mechanisms are differentially affected by these factors.

Coexistence mechanisms can be broadly classified as either stabilizing or equalizing (Chesson 2000, Adler et al. 2007). Stabilizing mechanisms rely on increased intraspecific compared to interspecific competition which relatively favors less abundant compared to more abundant species and thus facilitates the recovery of populations from low densities.

Equalizing mechanisms of coexistence rely on minimizing differences in average fitness. The debate over the relative importance of stabilizing and equalizing mechanisms in different communities is ongoing. Recently, Adler et al. (2007) argued that there is no clear-cut answer to the question of which mechanism structures a community. Rather, there are gradual transitions where either strong stabilizing mechanisms overcome large fitness differences, or weak stabilization is coupled with similar fitness between species (cf. Gravel et al. 2006; Chesson 2000b). For our analyses, we exemplarily chose one route to coexistence for each type of mechanism, respectively: (1) coexistence through over-compensating density regulation as a particular stabilizing mechanism where species differ only in one trait, namely their mechanism of density regulation; and (2) neutral coexistence of species with almost identical fitness and no stabilization. Below, we outline how each of these two example mechanisms theoretically operates under stable environments and indicate where they may be important in structuring real communities.

(1) Coexistence through over-compensation facilitates coexistence of two species on a single resource and results from a differentiation along an axis of density regulation mechanisms, from over-compensation towards under-compensation. With over-compensatory density regulation, individuals scramble for coveted resources and populations can exhibit cyclic or chaotic dynamics. With compensatory and under-compensatory density regulation, individuals follow strategies that effectively avoid resource over-use and lead to equilibrium dynamics. The interaction between two species, one an over-compensator and another with sufficiently different density regulation, results in temporally alternating community dynamics that allow recovery from low densities for both species: (a) The over-compensator tends to generate density fluctuations but is the inferior competitor at strong amplitudes of those fluctuations and (b) the competitor tends to dampen the over-compensators amplitudes when frequent but is inferior at weak amplitudes. In field studies, it is a challenging task to identify communities that rely (fully or partly) on this coexistence mechanism because the mechanism of density regulation is particularly difficult to estimate from field data (Godfray et al. 1990; Morris 1990). However, species that exert density regulation in early life-stages (and thus are most probable to over-compensate, Sinclair 1989) and live in highly diverse communities with apparently limited number of resources may depend critically on this mechanism. Examples may include the highly diverse small mammal and insect communities in some tropical rainforests where many species with no apparent differentiation in physiological characteristics or resource requirements coexist, or highly diverse marine

plankton communities that coexist on only a few potentially limiting resources (Huisman and Weissing 1999).

(2) Species that are equal in all aspects and compete with each other in a homogeneous landscape randomly drift to extinction (Gause 1934). According to Hubbell's neutral theory of biodiversity, this drift can be slow enough to maintain coexistence over very long time periods, particularly in situations with limited dispersal (Hubbell 2001). Hubbell's theory has been successful at reproducing empirically observed patterns of species richness (cf. Rosindell and Cornell 2007; e.g. tree diversity in tropical rain forests, Hubbell 2001; Hubbell 2006; species-abundance distributions in fynbos, Latimer et al. 2005; zooplankton diversity, Walker and Cyr 2007; and fish diversity, Etienne and Olff 2005) but has nevertheless been the subject of considerable debate as communities are very unlikely to be truly neutral (Gotelli and Mccabe 2002; Bell 2005; Walker 2007). This conflict has been partly resolved by the suggestion that neutral and niche theory are not mutually exclusive (Gotelli and Rohde 2002; Gilbert et al. 2006; Chesson 2000b). Even if local species' interactions exist some properties of a community may be insensitive to these interactions and can thus be adequately described by neutral processes (Bell 2005). Gotelli and Rohde (2002) concluded that presence-absence patterns for small-bodied taxa with low vagility and/or small populations (e.g. marine ectoparasites and herps) are mostly random, whereas those for large bodied taxa with high vagility and/or large populations (e.g. birds and mammals) are highly structured.

In this study, we utilize a spatially-explicit two-species metapopulation model to examine the impacts of patch isolation and geographic range-shifting due to climate change. We address three major research questions. First, what is the impact of patch isolation on the relative importance of neutral coexistence and stabilized coexistence in a fragmented but temporally stable landscape? Second, how do patch isolation and climate-induced range shifting -in isolation and combined- impair species assemblages? Third, do the two considered coexistence mechanisms respond differentially to changes in these environmental factors?

## 4.2 Model description

*Model description*

*Purpose and structure*

The model's purpose is to demonstrate effects of patch isolation and climate change on coexistence in a two species metapopulation. Species differ only in their density regulation. The model considers a landscape represented as a rectangular grid with habitat patches that are surrounded by matrix cells. It explicitly simulates the population dynamics of the two species in the habitat patches and models the dispersal of individuals between the patches. In each time step, local population dynamics with intra- and interspecific interactions are followed by dispersal.

*Local population dynamics*

Local population dynamics in each patch *i* are described by an extended version of the equation by Maynard Smith and Slatkin (1973; see also Hassell and Comins 1976):

$$N_{i,s}(t+1) \sim Pois\left( \frac{N_{i,s}(t) \cdot R_{sp}}{\left( \left( 1 + \left( R_{sp} - 1 \right) \left( \frac{N_{i,tot}(t)}{CC_i(t)} \right)^{b_s} \right) \right)} \right)$$

The population sizes on patch *i* of species *s* at time *t* is given by $N_{i,s}(t)$ and the species' maximum growth rate is given by $R_{sp}$ and was set to five which describes fast growth at low densities. Net population growth of both species is limited by the total number of individuals living on a patch and the current carrying capacity, $CC_i(t)$. We assume interspecific competition to be as strong as intraspecific competition, $N_{i,tot} = N_{i,A} + N_{i,B}$. Both species differ only in their mechanism of density regulation, which is characterized by $b_s$ ($b_s < 1$ corresponds to under-compensating, $b_s = 1$ to compensating, and $b_s > 1$ to over-compensating density regulation). This way, a wide range of combinations of density regulation mechanisms from under-compensation to strong over-compensation is comparable. We account for

demographic stochasticity by drawing random numbers from a Poisson distribution. We independently and randomly initialize populations for each species by drawing from a uniform distribution between *10* and *10+CC$_i$(t)* individuals.

*Dispersal*

In each time step, dispersal occurs after population growth. The population size after dispersal $N_i(t,d=1)$ is equal to the one prior to dispersal, $N_i(t,d=0)$, minus the number of emigrants, $N_{emi,i}(t)$, and plus the number of immigrants. The number of emigrants per patch is drawn from a binomial distribution with $N_i(t,d=0)$ number of trials and emigration rate $p_{emi}$. Emigration rate is constant over space and time and equal for both species. Species do not interact during dispersal. The number of immigrants from patch *i* to patch *j* is drawn from a multinomial distribution with $N_{emi,i}(t)$ trials and transfer probability $p_{ij}$. The matrix of transfer probabilities, with entries $p_{ij}$, describes the probability to move from patch *i* to patch *j*. Values decrease exponentially with the Euclidean distance between patches, $D_{ij}$, measured in units of grid cells:

$$p_{ij} = \frac{\exp\left(-\dfrac{1}{DD}D_{ij}\right)}{\sum\limits_{j}\exp\left(-\dfrac{1}{DD}D_{ij}\right)} \cdot \exp\left(-mD_{ij}\right)$$

The mean distance both species are able to disperse is defined by *DD* and the dispersal mortality rates are defined by *m*. The denominator scales the transfer probabilities $p_{ij}$ such that they add up to one over all *j* in the absence of dispersal mortality (for the special case *m=0*). The combined effect of *DD*, $p_{emi}$ and *m* defines the connectivity between the habitat patches; populations of species with long *DD*, high $p_{emi}$ and low *m* are well connected while populations of species with short *DD*, low $p_{emi}$ and high *m* are isolated.

*Simulation experiments*

We simulated two different scenarios: In the *fragmentation scenario* we addressed our first research question (What is the impact of patch isolation on the coexistence mechanisms in a temporally stable landscape?), whereas in the *climate change scenario* we focussed on the remaining two research questions (What is the impact of patch isolation and climate-induced range shifting on the coexistence mechanisms? Do the reactions of the mechanisms

differ?). The two scenarios differ in patch number, temporal stability of patches and species' dispersal abilities.

The landscape in the fragmentation scenario is a lattice of 20 by 20 cells. On the lattice two, four or eight habitat patches are distributed uniformly and randomly. Independently of the number of patches the global amount of available habitat is held constant (total carrying capacity of the landscape is set to 500 individuals). Thus, local carrying capacities decrease with increasing patch number (250, 125 or 63 individuals, cf. Tab. 4.1) and are constant over time. We investigated isolation effects by comparing different dispersal abilities: species with long distance dispersal and no dispersal mortality (*DD=20* and *m=0*) and species with short distance dispersal and severe dispersal mortality (*DD=1* and *m=0.2*). In total, we conducted 541,800 simulations for the fragmentation scenario: three different patch numbers times two connectivity levels times 903 combinations of density regulation mechanisms (triangular matrix with diagonal and 43 different density regulation mechanisms: 42*43/2) times 100 repetitions.

**Table 4.1:** Description of parameters that varied across simulation experiments, parameters that were kept constant across all simulation experiments, and output variables

| **Parameters that varied across simulation experiments** | | | |
|---|---|---|---|
| *Symbol* | *Parameter* | *Structure or process* | *Values* |
| $L_{Size}$ | Lattice size [cells$^2$] | Landscape: structure | 20*20 vs. 40*240 |
| $P_{Number}$ | Patch number | Landscape: structure | 2,4,8,90 |
| $CC_i$ | Local carrying capacities | Landscape: patch growth | 63, 125, 250, 500 |
| $b_s$ | Density dependence parameter | Reproduction | [$e^{-2}$; $e^2$], in steps of $e^{0.1}$ |
| $DD$ | Mean dispersal distance [cells] | Dispersal | 1,2,6,12,20 |
| $m$ | Dispersal mortality rate | Dispersal | 0,0.2 |
| $p_{emi}$ | Emigration rate | Dispersal | 0.01,0.1 |
| $CW_{width}$ | Climate window-width [cells] | Landscape: climate change | 20,40 |
| $CW_{speed}$ | CW-speed [cells/timestep] | Landscape: climate change | 0.5,1,2,4,8 |
| **Parameters that were kept constant across all simulation experiments** | | | |
| *Symbol* | *Parameter* | *Structure or process* | *Values* |
| $R_{sp}$ | Growth rate of species | Reproduction | 5 |
| $R_p$ | Growth rate of patches | Landscape: patch growth | 5 |
| $CC_{max}$ | Maximum carrying capacity | Landscape: patch growth | 500 |
| **Output variables** | | | |
| *Symbol* | *Variable* | | |
| CPR | Coexistence probability | | |
| CPO | Coexistence potential | | |

The landscape in the climate change scenario is a lattice 240 cells in width by 40 cells in height with 90 potential habitat patches distributed uniformly and randomly across it. Local carrying capacities are dynamic in the sense that not all 90 potential habitat patches provide

resources in each time step but only those patches within a 'climate window' (Travis 2003; Best et al. 2007). This climate window has a certain width, $CW_{width}$, and moves across the landscape over time. The number of cells the window moves per timestep is defined as the rate of range shifting, $CW_{speed}$ (Fig. 4.1). Initially, the window is located at the left hand side of the landscape and remains stationary for the first 100 timesteps. In the stationary period, all carrying capacities within the window are set to the maximum carrying capacity (patches can sustain a population), outside all carrying capacities are set to zero (patches cannot sustain a population).
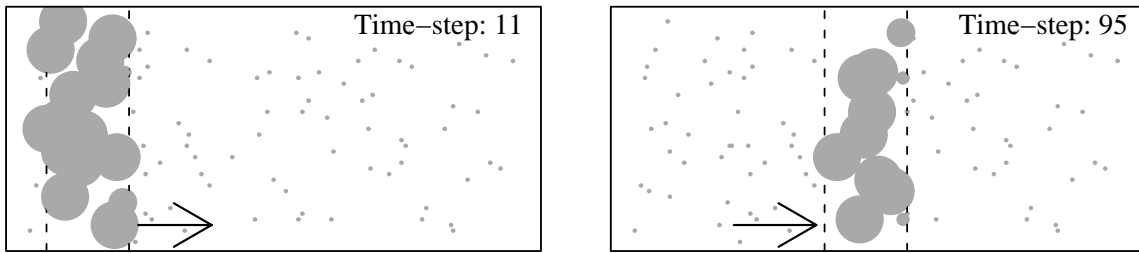


**Figure 4.1:** When the climate window moves across the landscape (shown are snap-shots from timesteps 11 and 95), potential habitats (grey dots; diameters correspond to sizes of carrying capacity) gradually become suitable for the two species; once the window has moved past a habitat patch, the carrying capacity immediately goes down to zero and the local populations go extinct.

After the stationary period, the window starts moving to the right hand side of the landscape and stops only after reaching the border of the landscape. Potential habitats entering the window gradually become suitable for the species, potential habitats leaving the window instantly loose their suitability and local populations go extinct. The local carrying capacity of a patch, $CC_i(t)$, upon entering the window is set to a value of one individual and its temporal development is governed by the equation of Maynard Smith and Slatkin (1973):

$$CC_i(t+1) = \frac{CC_i(t) \cdot R_p}{1 + (R_p - 1)CC_i(t)/CC_{max}}$$

The patch growth rate, $R_p$, determines how quickly patches become suitable once entering the climate window. We assumed fast growth ($R_p$=5). The maximum carrying capacity, $CC_{max}$, was set to 500 individuals. Patch dynamics occur in each time step and are followed by local population dynamics and dispersal. We investigated climate change via increasing rates of range shifting ($CW_{speed}$=0.5, 1, 2, 4, 8) and different sizes of the climate window ($CW_{widths}$=*20* or *40*; cf. Tab. 4.1). We analysed isolation effects comparing different dispersal distances ($DD$=1, 2, 6, 12, 20) and emigration rates ($p_{emi}$=*0.01 or 0.1*; cf. Tab. 4.1). In total we conducted 9,030,000 simulations for the climate change scenario: two climate window sizes times two emigration rates times five rates of climate change times five dispersal distances times 903 combinations of density regulation mechanisms times 100 repetitions.

The simulation model is implemented with the Borland C++ Builder 5, random number distributions are taken from the GNU Scientific Library (GSL Team 1992), and graphics are created with R 2.6.1 (R Development Core Team 2007).

### *Aggregated output variables*

To facilitate the comparison between equalizing and stabilizing mechanisms we aggregated the information from time-series of species' abundances (Fig. 4.2a) in two measures, the coexistence probability (Fig. 4.2b) and the coexistence potential (Fig. 4.2c).

#### *Coexistence probability, CPR*

Firstly, we aggregated 100 replications of one combination of density regulation mechanisms into an estimate of the probability for the two species to still coexist in the landscape after 1000 years. We repeated this procedure for different combinations of density regulation mechanisms ranging from under- to strong over-compensation. The species were identical in all other traits. We plotted the *CPR* of the possible combinations of density regulation mechanisms in a triangular matrix to illustrate the parameter window of coexistence (Fig. 4.2b, the grey shading codes *CPR* for different combinations of $b_s$-values).

#### *Coexistence potential, CPO*

Secondly, we aggregated the size (i.e. the number of parameter combinations) and the strength (i.e. the coexistence probability) of the parameter window of coexistence in a new output variable called coexistence potential, *CPO*, and assumed that both size and strength of the window characterized the overall likelihood of coexistence. We argue that the more parameter combinations result in coexistence and the higher the probability to coexist, the

more likely it is that a favourable combination of density regulation mechanisms evolves in an ecosystem. Thus, we measured the coexistence potential, *CPO*, by summing up all coexistence probabilities for all different combinations of density regulation mechanisms. We repeated this procedure for different fragmentation and climate change regimes (Fig. 4.2c).
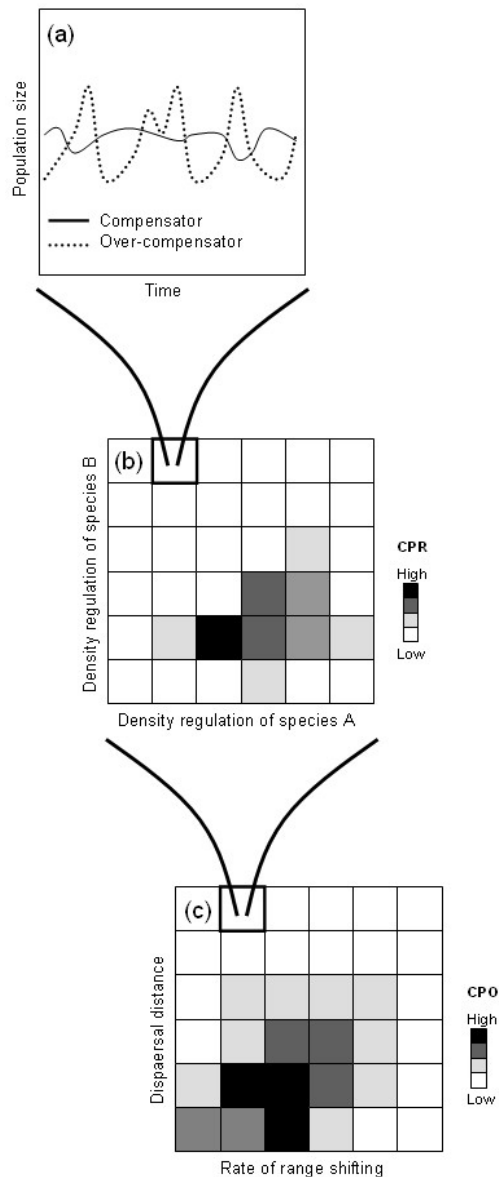


**Figure 4.2:** The measures of coexistence probability, *CPR*, and coexistence potential, *CPO*, were derived in two aggregation steps: In a first step we calculated the probability of coexistence after 1000 years, by aggregating 100 repetitions of time series (panel a) for each combination of density regulation values (panel b). In a second step, the sum of coexistence probabilities of all cells in b was calculated and plotted in the corresponding cell of c (note the different axes in panels b and c).

## 4.3 Results

Our first research question focussed on the impact of patch isolation on the relative importance of two coexistence mechanisms in a temporally constant but spatially fragmented landscape (fragmentation scenario). In a first step, we analysed the distinctiveness of our aggregated measures with regard to the two coexistence mechanisms, neutral coexistence and stabilized coexistence. We plotted the coexistence probability against the different combinations of density regulation. We found two distinct and cohesive regions of parameter combinations that led to coexistence (Fig. 4.3). Coexistence probability was high either if species displayed moderate dissimilarities in their density regulation, i.e. one species with over-compensation and the other different (e.g. Fig. 4.3b, stabilized coexistence along the negative diagonal), or if species showed equal or very similar density regulation (e.g. Fig. 4.3d, neutral coexistence along the positive diagonal). The coexistence potential displayed a distinct depression at the $b$-ratio ($b_A/b_B$) of $e^{0.6}$~1.82 and local maxima below as well as above this value. Based on this result we defined that neutral coexistence corresponded to $b$-ratios below 1.82 while stabilized coexistence corresponded to $b$-ratios above 1.82. (cf. grey vertical bar in Fig. 4.4b). In a second step, we examined the influence of patch isolation. We could identify distinct differences between the two coexistence mechanisms. Stabilized coexistence was strong and robust in a landscape with two patches, no matter whether they were well connected or isolated ($DD$=20 and $m$=0, Fig. 4.3a, b). With an increasing number of patches, local carrying capacity decreased and fewer combinations of density regulation mechanisms resulted in stabilized coexistence, especially if patches were isolated (Fig. 4.3c, d).

In contrast, neutral coexistence only occurred if patches were isolated ($DD$=1 and $m$=0.2, Fig. 4.3b, d, f). The higher the number of patches, the more combinations of density regulation mechanisms could coexist and the less similar species needed to be. On eight well-connected patches, coexistence was not possible at all (Fig. 4.3e). However, on eight isolated patches both coexistence mechanisms could result in persistence (Fig. 4.3f). In summary, stabilized coexistence dominated in landscapes with either a low number of patches (two connected or isolated patches, Fig. 4.4) or in landscapes with a greater number of strongly connected patches with moderate carrying capacities (four connected patches, Fig. 4.4 a, c).
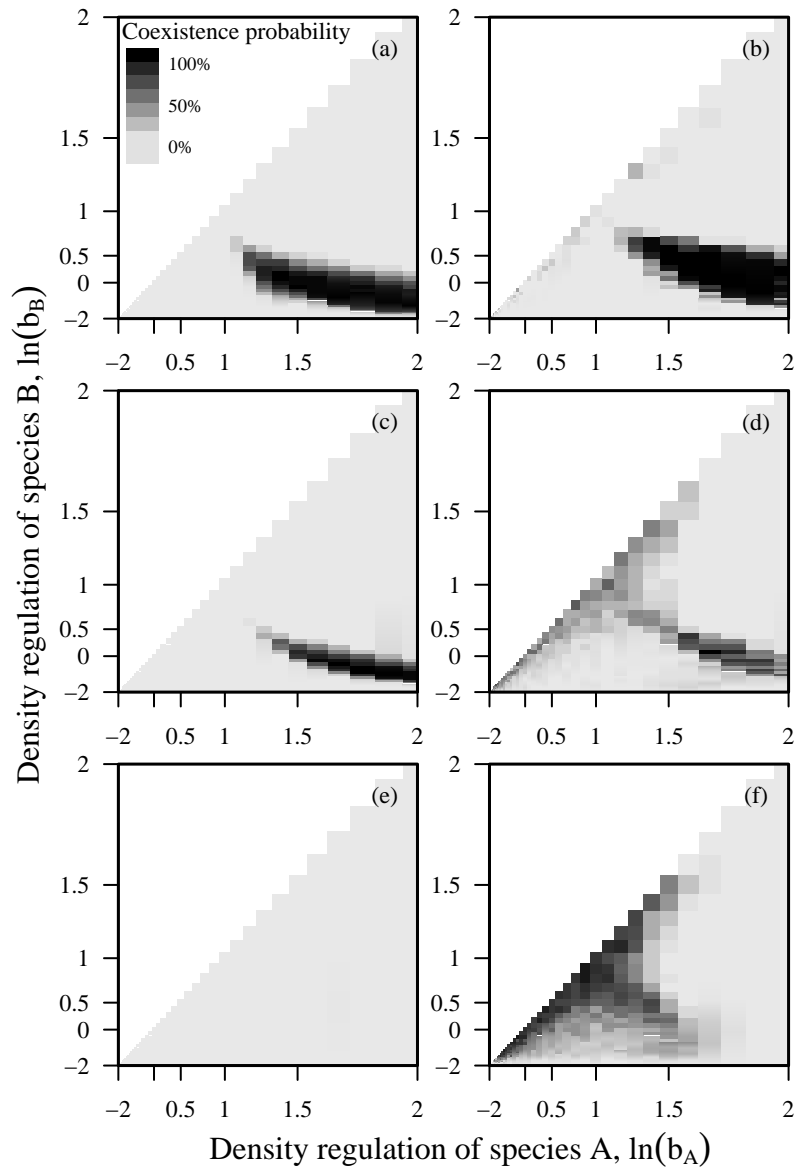
**Figure 4.3:** Coexistence probability of two species that differ only in their mechanism of density regulation (ln(b)<0: under-compensation, ln(b)=0: compensation, ln(b)>0: over-compensation) over 1000 time steps; (a), (c), and (e) with high connectivity (mean dispersal distance: 20 cells and no dispersal mortality) between 2, 4, and 8 patches and (b), (d), and (f) with low connectivity (mean dispersal distance: 1 cell and severe dispersal mortality) between 2, 4, and 8 patches; darker colours indicate higher coexistence probability, white: no simulations.
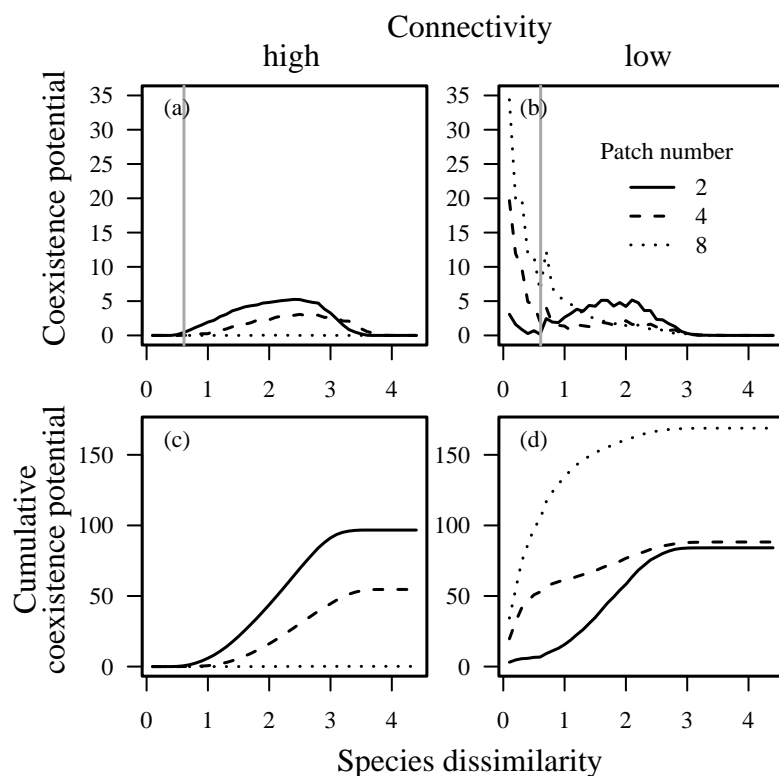
**Figure 4.4:** Coexistence potential against dissimilarity of two species; (a), and (c) with high connectivity (mean dispersal distance: 20 cells and no dispersal mortality) between 2, 4, and 8 patches and (b), and (d) with low connectivity (mean dispersal distance: 1 cell and severe dispersal mortality) between 2, 4, and 8 patches; grey vertical line indicates the selected criterion for separation of the two coexistence mechanisms.

Neutral coexistence dominated in landscapes with isolated patches and especially if the number of patches was high (Fig. 4.4b, d). However, species with moderate dissimilarities, i.e. those at the intersection of stabilized coexistence and neutral coexistence, were able to coexist on four or eight isolated patches, indicating that here both mechanisms acted in concert to facilitate coexistence.

Within our second research question, we investigated how patch isolation and range shifting impaired species assemblages both separately and in combination (climate change scenario). In general, increasing rates of climate-induced range shifting as well as increasing patch isolation (through reduced dispersal distances) strongly decreased coexistence (Fig. 4.5). Severe impacts on coexistence occurred even under very moderate rates of climate change. Further increasing the rate of climate change did result in a greater impact but most of the damage was already done by the lower rate. For increased patch isolation, an intermediate range of dispersal distances was most sensitive to a further decrease. Species with low

emigration rates and narrow climate windows were most vulnerable to climate change and patch isolation such that already very slow rates of range shifting disrupted the coexistence mechanisms completely. Halving the width of the climate window reduced coexistence potential by a third (Fig. 4.5a, c vs. 4.5b, d) and a tenfold increase in emigration rates (from 0.001 to 0.01) doubled the coexistence potential (Fig. 4.5a, b vs. 4.5c, d). Thus, a strong decrease in the climate window size, i.e. in the range size, could partly be buffered by high emigration rates.
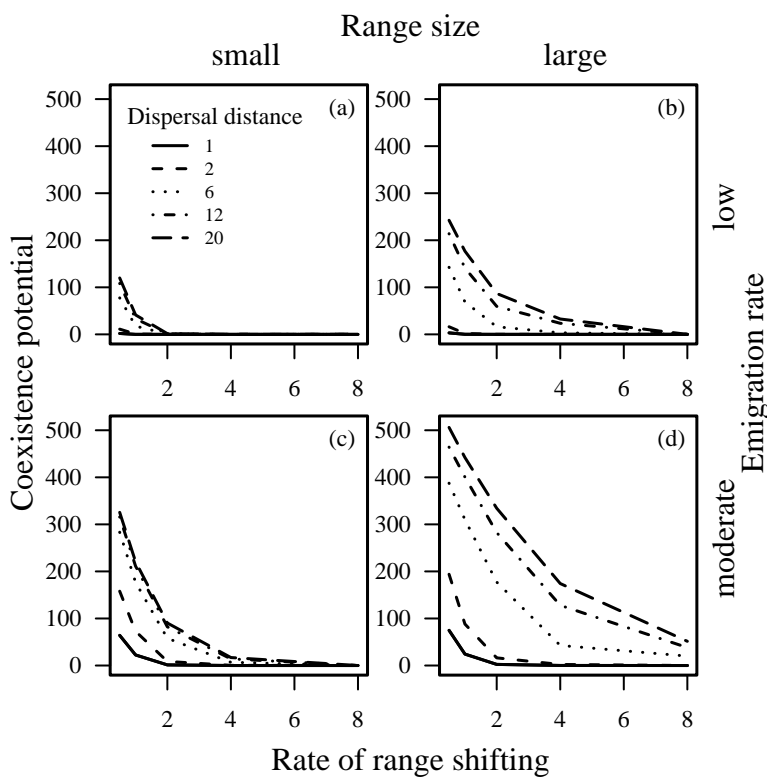
**Figure 4.5:** Coexistence potential against rate of range shifting during climate change for decreasing dispersal distances; (a), and (c) small climate window ($CW_{width}=20$ cells) and (b), and (d) large climate window ($CW_{width}=40$ cells); above: low emigration rate ($p_{emi}=0.01$), below: high emigration rate ($p_{emi}=0.1$).
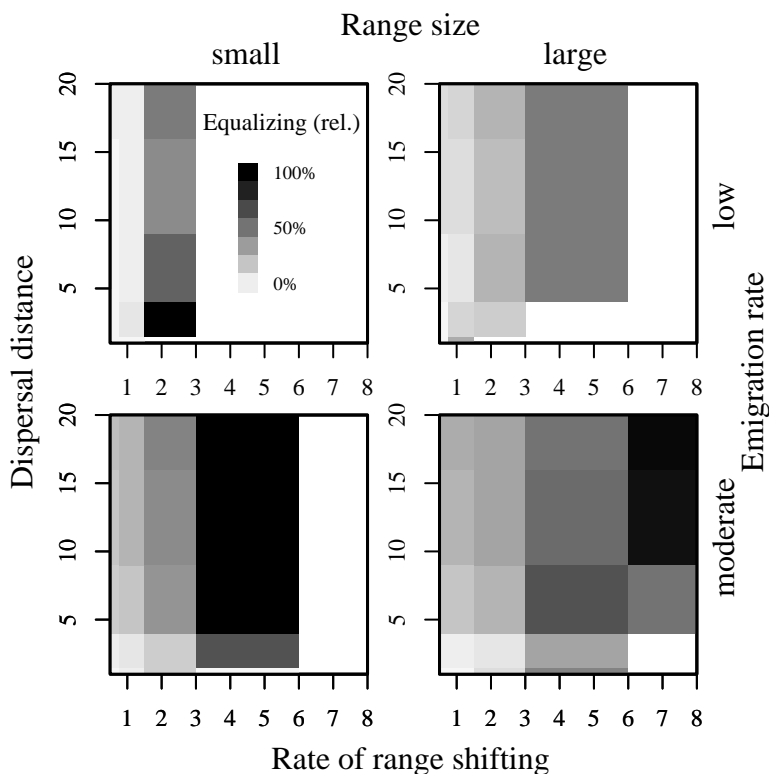
**Figure 4.6:** Fraction of neutral coexistence in overall coexistence potential for increasing rates of range shifting and decreasing dispersal distances; (a), and (c) small climate window ($CW_{width}=20$ cells) and (b), and (d) large climate window ($CW_{width}=40$ cells); above: low emigration rate ($p_{emi}=0.01$), below: high emigration rate ($p_{emi}=0.1$); white cells: overall coexistence potential equals zero.

For our third research question we investigated whether the two coexistence mechanisms responded differentially to patch isolation and climate change (climate change scenario). Remarkably, the above described general impacts of climate change and patch isolation did not apply equally to both coexistence mechanisms: Under most conditions, coexistence potential was higher for stabilized coexistence than for neutral coexistence (Fig. 4.6). However, certain landscape conditions existed where only one or the other mechanism facilitated coexistence under environmental change: Only stabilized coexistence was able to cope with a combination of strong isolation and slow climate change, and only neutral coexistence was able to follow quick rates of changing climate. In general, the relative dominance of neutral coexistence increased with accelerated climate change and decreased with decreasing dispersal distances (Fig. 4.6). Thus, increasing isolation had a greater impact on neutral coexistence while stabilized coexistence was more sensitive to climate change.

## 4.4 Discussion

Here, we have taken some initial steps towards understanding how the nature of the mechanisms involved in structuring communities may determine how those communities will respond to one, or more, environmental drivers. There has been considerable recent debate over the relative roles of stabilizing and neutral mechanisms in structuring communities and a growing body of theory addresses how these alternative mechanisms operate on temporally and spatially heterogeneous landscapes (Chesson 2000b; Gotelli and Mccabe 2002; Adler et al. 2007). Our work highlights that understanding the nature of coexistence has considerable potential implications for predicting and managing the consequences of environmental change on biodiversity.

Building on the framework of equalizing and stabilizing mechanisms (Chesson 2000b; Adler et al. 2007) we analyse one example coexistence mechanism of each category: Stabilized coexistence through over-compensation is known to work in homogeneous and stable landscapes. However, our results demonstrate that it is not restricted to these landscapes. It also operates in fragmented landscapes if either local carrying capacities are high or patches with moderate carrying capacities are well connected (Fig. 4.3). High carrying capacities and good connectivity are essential because stabilized coexistence depends on endogenously generated density fluctuations. Mean population densities need to be high to allow for sufficient amplitudes of these fluctuations without risking stochastic extinctions in times of density depressions. However, detrimental effects of only low to moderate carrying capacities can be buffered by high patch connectivity and thus tightly coupled local population dynamics. In landscapes with a combination of low local carrying capacities and isolation, coexistence may occasionally occur but it is rare. In these cases the coexistence mechanism breaks down locally but community dynamics are spatially uncorrelated. Thus, species may re-immigrate from neighbouring patches, and slow down regional extinction (Fig. 4.3f). The neutral mechanism only promotes long-term coexistence in fragmented landscapes with a sufficient number of weakly connected patches (Fig. 4.3f). In such landscapes, limited dispersal slows down the drift to competitive exclusion (Roy et al. 2004). Recently, Wang et al. (2005) claimed that this result is only an artefact and critically depends on the assumption that extinction and colonization parameters are independent of the relative abundances of both species in commonly occupied patches. They state that this oversimplified assumption would give an unfair advantage to regionally rare species. However, our results

demonstrate that coexistence does occur even with explicit consideration of local population dynamics, which automatically includes abundance dependent local extinction and re-colonization processes.

The framework of equalizing and stabilizing mechanisms classifies coexistence mechanisms depending on dissimilarities between species (Adler et al. 2007). Our approach of coexistence along a gradient of density regulation mechanisms relates well to this framework as changes in a single species' trait (the density regulation mechanism) led from neutral to stabilized coexistence. Consequently, dissimilarity can be measured on a one-dimensional scale. With increasing dissimilarity in density regulation, neutral coexistence decreases and stabilized coexistence increases. The turnover from neutral coexistence to stabilized coexistence is gradual, with both mechanisms contributing to the overall coexistence potential at moderate species differences (Figs. 4.3, 4.4). The relative contribution of the mechanisms to overall coexistence depends on patch isolation and patch size: The stabilizing mechanism dominates homogeneous landscapes or landscapes with large and strongly connected patches whereas the neutral mechanism dominates fragmented landscapes with small habitat patches. Both mechanisms co-occur in landscapes with intermediate patch isolation and patch size.

A growing body of literature demonstrates that climate change and patch isolation severely reduce species survival (e.g. Sala et al. 2000; Travis 2003; Thomas et al. 2004; Best et al. 2007). What is new in our study is the focus on community structure i.e. on differential responses of assemblages persisting through alternative coexistence mechanisms. Comparable to species survival, species coexistence strongly suffers from climate change and patch isolation. Remarkably, climate change already imposes severe impacts at low rates of range shifting in fragmented landscapes. This implies that communities may undergo rapid changes already in initial periods of climate change leaving management actions little time to mitigate detrimental impacts on biodiversity. We show that at the community level, the response to climate change and patch isolation sensitively depends on the underlying coexistence mechanisms. Communities with neutral coexistence are much more sensitive to increasing patch isolation than communities with stabilized coexistence. Although neutral communities depend on moderately isolated local population dynamics and go extinct in homogeneous or well-connected landscapes, they severely suffer from very strong isolation. This is because neutral coexistence critically relies on sufficient re-immigration to balance local drifts to extinction. Conversely, communities with stabilized coexistence are much more sensitive to

climate change than neutral communities. Stabilized communities can track even low rates of climate change only if the number and size of local habitat patches are sufficiently large and well connected. The reason is that this coexistence mechanism relies on large mean population densities to buffer depressions during density fluctuations (Fig. 4.6). Under climate change, however, new patches and new populations constantly need to establish when entering the climate window and are therefore on average smaller. At high rates of climate change, local populations or even patches may never reach their potential size before the climate window passes. In real ecosystems, this problem becomes important when resources need a long time to establish, e.g. for species communities depending on mature forests or on upland moors. Species with small dispersal ranges and/or low emigration rates are especially vulnerable because they reach newly established patches with a delay. For them, already slow climate change may lead to extinction. These added mortality effects reduce single species persistence but are amplified when communities depend on well-balanced dynamics between competing species.

It is clear that a greater understanding of the mechanisms that structure communities would improve our ability to predict how species' will respond to environmental change, and we suggest that future work focussing in three areas would be beneficial. First, there is a clear need to validate our theoretical findings using data on real communities. Unfortunately, to date there is a rather small number of field studies that have investigated the community-level responses to patch isolation or climate change independently, let alone considering potentially synergistic effects. In general, published studies in this area confirm our finding that accelerating climate change and strong patch isolation threaten communities (Wilson et al. 2007; Echeverria et al. 2007; Manu et al. 2007; Benedick et al. 2006; Burke and Goulet 1998). Future field studies should aim to identify interactions between environmental drivers and ideally also seek to establish how communities structured by the different mechanisms may be differentially impacted. Establishing field studies to validate the predictions of models such as that presented in this paper can be challenging. We agree with Benton et al. (2007) that taking a microcosm approach may offer considerable potential, at least as a complementary approach. Therefore, our second recommendation is that a number of different microcosm communities comprising a wide range of species from different taxa should be established with a view to investigating the range of community-level responses when those communities are subjected to environmental perturbations. As Benton et al. (2007) argued there can be considerable benefits to be gained from replicating experiments

across a range of analogue model systems. In this case, it would provide an excellent opportunity to establish how well results from one community are likely to generalise across other communities. Third, further theoretical work is necessary to consider both other climate change effects, e.g. the impact of altered disturbance regimes (Easterling et al. 2000; Beniston et al. 2007; Johst and Huth 2005), and further stabilizing mechanisms. These extensions would also enable us to ask new questions regarding the formation of novel assemblages during climate change with characteristics different from those under stable climate.

We conclude that climate change and strong patch isolation generally impair communities but act differentially with respect to the underlying coexistence mechanisms. Monitoring data that ignore these processes and only focus on single species abundances are prone to producing contradictory and incomprehensible results, with the same changes in environmental conditions resulting in extinction in one community but not in the other. Therefore, a profound analysis of coexistence processes that structure the community under constant conditions is pivotal to understand how a community will react to changing conditions. Based on this understanding we can improve both the predictions of impacts of environmental changes on communities and the development of management and conservation plans. Our results suggest that adaptations to climate change may have to be differentiated according to the community structure.

# 5 Neutral vs. niche-based coexistence: Combining field data and mechanistic modelling to explain community functioning of neotropical small mammals

There is an increasing recognition that interspecific interactions play a key role in determining the response of species' communities to anthropogenic landscape fragmentation. Interactions of species competing for similar limiting resources can operate via neutral and niche-based processes to promote coexistence. Here, we investigated the relevance of these two broad classes of coexistence processes for the functioning of a small mammal community in the remnants of the Brazilian Atlantic rainforest.

Considering interspecific interactions, disturbances and dispersal, we built a mechanistic simulation model to calculate population dynamics of the eighteen most abundant species in the community. We estimated lower-level process parameters in the model using large scale field data and recent advances in Bayesian statistics. Parameter estimates highlight the importance of interspecific interactions for small mammal community dynamics. Niche-based processes dominate interactions of species using different levels of vertical forest structure whereas neutral processes dominate interactions of species sharing a common level of vertical stratification. The analyses of the diversity patterns on local and regional scales support this finding. Based on this increased understanding of community dynamics we were able to investigate broad-scale and long-term effects of the current fragmentation pattern and found that it implies a future increase in heterogeneity of biodiversity for the small mammal community.

We propose that a combined approach of Bayesian statistics and mechanistic modeling provides a convenient framework for determining interspecific interaction strengths and thus for differentiating between neutral versus niche-based mechanisms of coexistence. As interspecific interactions are decisive for the functioning of a specific community and its response to landscape changes, these analyses further our understanding of observed biodiversity patterns and may allow us to reveal otherwise unnoticed threats.

# 5.1 Introduction

Anthropogenic landscape fragmentation occurs at ever increasing rates and causes population decline and species extinctions across the globe (Sala et al. 2000; Thomas et al. 2004; Bugmann 2003). The great majority of work devoted to understanding the ecological processes underlying fragmentation impacts on species survival has focused on single species approaches, e.g. by applying viability and metapopulation analyses to flag-ship species (e.g., Hanski 1999; Bascompte and Solé 1995; Frank 2005; Drechsler and Wissel 1997; Münkemüller and Johst 2006; Münkemüller and Johst 2007; Brito and da Fonseca 2007). Based on these analyses, ecologists prioritize conservation actions such as increasing the number of corridors (e.g., Frank 2004) or reducing disturbance frequency (e.g., Carroll and Miquelle 2006; Sachot et al. 2006; Frank et al. 2002; Johst and Drechsler 2003; Johst and Huth 2005). The reasoning behind this is that other species in the community will be conserved along with the flag-ship species (Fisher 1998). However, there is an increasing recognition that single species approaches alone are insufficient to preserve whole communities. Neglecting properties of the accompanying species and interactions among them may bias analyses and thus lead to inaccurate conclusions regarding the impact of environmental change and landscape fragmentation (Guisan and Thuiller 2005; Heikkinen et al. 2006; Araujo and New 2007; Brooker et al. 2007).

One important type of species interactions is competition for limiting resources. For these communities, niche differentiation has long been suggested as the only way to reduce competitive exclusion and to allow species to coexist (Lotka 1925; Volterra 1926). Niche based coexistence relies on differences in traits that increase intraspecific compared to interspecific competition and cause species to limit their own populations more than they limit others (Chesson 2000b). Recently, a competitive explanation for the maintenance of biodiversity was brought up. Neutral theory challenges the niche paradigm by proposing that species similarities and not their differences explain high biodiversity in many natural communities (Bell 2000; Hubbell 2001). The central assumptions of neutral theory are that all species are identical in their effects on one another and that stochasticity, i.e. random variation in births, deaths and dispersal, is the only driver of trends in population dynamics. These stochastic events eventually drive all but one species extinct. However, if extinction rates are slow, speciation occurs and dispersal between subpopulations is limited, high diversity can be maintained over long time periods.

The debate over the relative importance of niche differentiation and neutral processes for natural communities is considerable (Adler et al. 2007). Great evidence exists for species' niche differences and their coexistence-promoting effect (Reineking et al. 2006; reviewed in Rees et al. 2001), but only few studies have been able to demonstrate their importance for the diversity we observe in nature (Silvertown 2004; Adler et al. 2007). Neutral theory has been successful at reproducing empirically observed patterns of species richness (Rosindell and Cornell 2007; Hubbell 2006; Latimer et al. 2005; Etienne and Olff 2005; Walker and Cyr 2007), but it has nevertheless been the subject of criticism as communities are very unlikely to be truly neutral (Gotelli and Mccabe 2002; Bell 2005; Walker 2007). This conflict has been partly resolved by the suggestion that neutral and niche theory are not mutually exclusive but complement each other (Chesson 2000b; Bell 2005; Adler et al. 2007).

An evaluation of how these processes structure communities is required if we are to better understand the potential threats of fragmentation for biodiversity. However, much needed community approaches are hampered by the fact that critical information such as life history traits, or detailed and fine scale information on individual and species interactions, which would allow for a mechanistic understanding of ecological processes, are often limited (Brito 2004). These data are difficult to collect and thus are often available only for a few well investigated species, while for other species in the community the data are too incomplete to be easily incorporated in traditional analyses of species requirements and risk assessments. Ecological data that are more widely available are collected at broader spatial scales and represent simple counts of individuals or records of species presence. Information about the underlying processes of community dynamics is 'hidden' in these data. Thus, techniques that help utilizing these data to reveal the underlying processes are a key for analysing the interactions and dynamics of multi-species systems (Burnham and Anderson 1998; Grimm et al. 2005).

One approach to this problem is to use inverse modelling, i.e. to implement mechanistic models that simulate the hypothesised underlying processes directly, and to fit them to the broad-scale ecological data (Burnham and Anderson 1998; Henle et al. 2004; Grimm and Railsback 2005). In contrast to traditional regression models, these models have the potential to enhance our understanding of ecological interactions, to allow for generalizations beyond the specific situation of the data setting, and to be able to estimate future developments (Wissel 1989; Grimm and Railsback 2005). However, the challenge associated with

mechanistic models lies in the process and parameter uncertainty. In particular, low level system processes are often unavailable or cannot be estimated from field studies.

Here, we apply a mechanistic simulation model to better understand the impacts of forest fragmentation on the highly diverse small mammal community of the Brazilian Atlantic forest, one of the five most important biodiversity hotspots of the world (Myers et al. 2000; Brito 2004). The model output is confronted with count data collected for 18 species of small mammals across 18 forest patches. Estimation of the parameters for the low level system processes in the model builds upon recent advances in Bayesian statistics (Van Oijen et al. 2005). With the parameterized mechanistic model, we first investigate whether neutral and/or niche-based processes govern the community dynamics of the small mammals: Do species differ in fitness-related traits? How strong is competition between species? Are all species identical in their effects on one another? Secondly, we analyse spatio-temporal population dynamics and estimate long-term effects of the current fragmentation regime on biodiversity. Finally, we quantify the differences between the mechanistic approach and a traditional regression analysis that does not consider interspecific interactions.

## 5.2 Study system and data compilation

Despite its great importance for the maintenance of biodiversity, the Atlantic forest is one of the most endangered ecosystems worldwide. Today, less than 8% of the original forest cover is left. Conservation strategies for this ecosystem depend on information about how biodiversity is maintained and affected by increasing habitat loss and isolation. Small mammals, i.e. rodents and marsupials, provide a good study system for contributing to this question. They play an important ecological role in the forest as they influence forest regeneration through seed and seedling predation (Pizo, 1997; Vieira et al., 2003a) and seed dispersal (Grelle and Garcia, 1999; Vieira and Izar, 1999; Pimentel and Tabarelli, 2004). Most importantly, these animals clearly respond to habitat and landscape changes: The abundance of several species is affected by foliage density and vertical stratification (Malcolm, 1995; Gentile and Fernandez, 1999; Pardini, 2001; Grelle, 2003) and with few exceptions, the great majority of species avoids dispersal through open habitats (Stallings, 1989; Stevens and Husband, 1998; Feliciano et al., 2002; Pires et al., 2002).
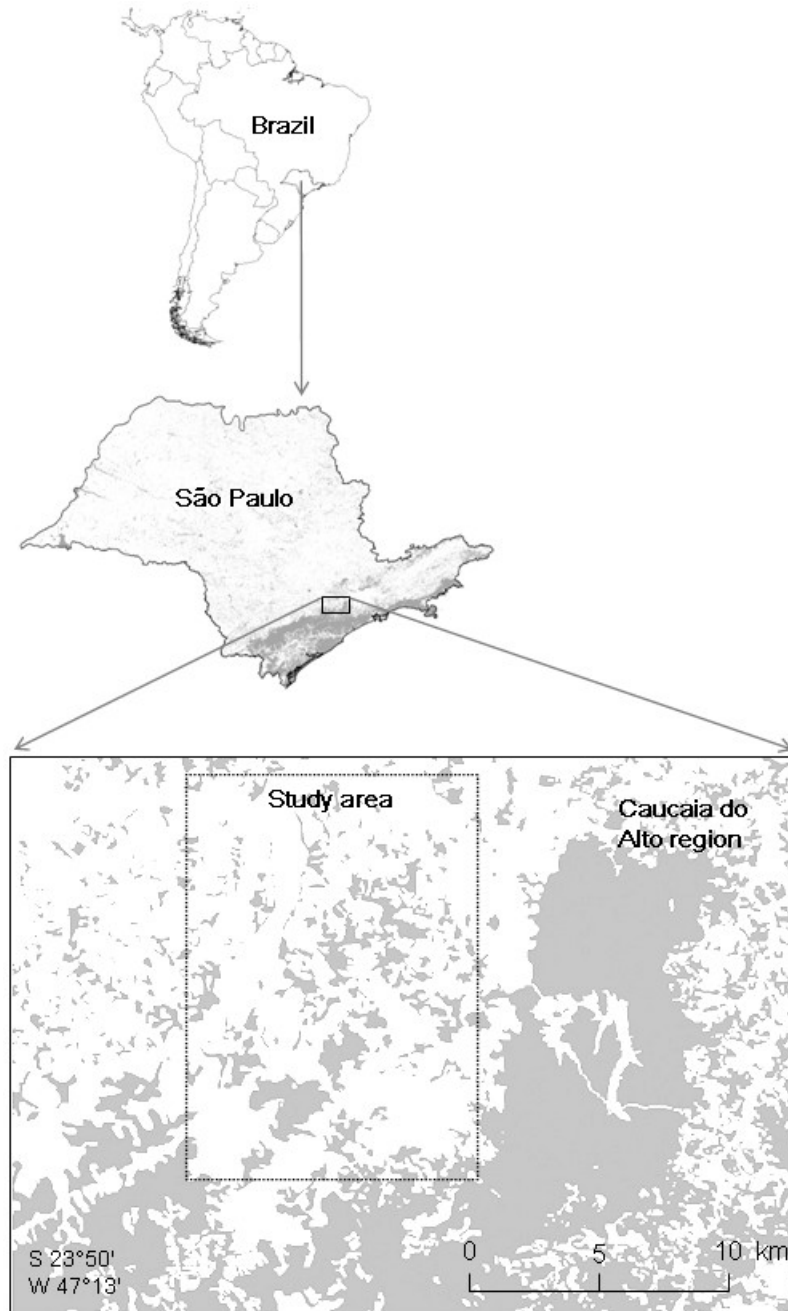
**Figure 5.1:** Maps showing the distribution of current remnants of Atlantic Forest (grey shaded) in the study area located in the Caucaia do Alto region in the State of São Paulo, Brazil.

Our study area is located in Caucaia do Alto in the State of Sao Paulo, Brazil (Fig. 5.1). The region is homogeneous in terms of climate, altitude and forest types. Monthly mean temperature ranges from 11 to 27°C, rainfall is around 1300 to 1400 mm/year, and altitude varies from 850 to 1100 m. The landscape is dominated by open habitats (58%) and native

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secondary forest (31%, Fig. 5.2). The forest is a transition between the coastal Atlantic rain forest and the Atlantic semi-deciduous forest. It can be classified as 'Lower Montane Atlantic Rain Forest' (Oliveira-Filho and Fontes, 2000).
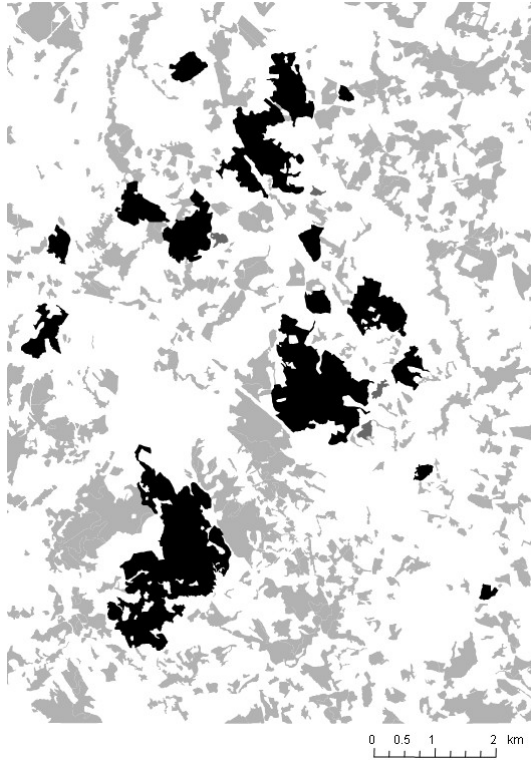


**Figure 5.2:** Map of the study area with investigated forest fragments (black), forest fragments (grey) and matrix (white).

The predominant matrix habitats, i.e. the open habitats surrounding the forest patches, are agricultural areas (38%), urban or rural areas with buildings (14%), native vegetation in early stages of regeneration (7%) and homogeneous plantations of pine or eucalyptus (7%). The highly diverse small mammal community in this region consists of marsupials and rodents and can be grouped based on their vertical stratification, i.e. their mainly occupied layer of the forest: terrestrial, scansorial, and arboreal species. The transition between scansorial and arboreal species is gradual. Therefore, we comprise them in a single group which we refer to as scansorial species in the following.

**Table 5.1:** Overview of investigated species community and species attributes (vertical stratification, classification and matrix intolerance, $MI_s$).

| Name | Vertical stratification | Classification | $MI_s$ |
|---|---|---|---|
| *Oligoryzomys nigripes* | terrestrial | rodent | 0.57 |
| *Marmosops incanus* | scansorial | marsupial | 0.99 |
| *Akodon montensis* | terrestrial | rodent | 0.00 |
| *Delomys sublineatus* | terrestrial | rodent | 0.98 |
| *Oryzomys angouya* | scansorial | rodent | 0.96 |
| *Didelphis aurita* | scansorial | marsupial | 1.00 |
| *Monodelphis americana* | terrestrial | marsupial | 1.00 |
| *Brucepattersonius soricinus* | terrestrial | rodent | 0.99 |
| *Oryzomys russatus* | terrestrial | rodent | 1.00 |
| *Gracilinanus microtarsus* | scansorial | marsupial | 1.00 |
| *Thaptomys nigrita* | terrestrial | rodent | 0.99 |
| *Juliomys pictipes* | scansorial | rodent | 0.95 |
| *Oxymycterus dasytrichus* | terrestrial | rodent | 1.00 |
| *Phillomys nigrispinus* | scansorial | rodent | 1.00 |
| *Monodelphis macae* | terrestrial | marsupial | 1.00 |
| *Philander frenata* | scansorial | marsupial | 1.00 |
| *Bibimys labiosus* | terrestrial | rodent | 1.00 |
| *Marmosops paulensis* | scansorial | marsupial | 1.00 |

Our analysis of fragmentation impacts was built on a dataset composed of counts of 18 small mammal species, terrestrial and scansorial species, that occupy forest habitats in 18 patches of different size and with different degrees of isolation (Pardini et al. 2005), a further dataset on counts of the small mammals in the matrix between the forest patches (Umetsu and Pardini 2007) and information on species and landscape characteristics derived from the literature, expert knowledge and a GIS map (Fig. 5.2, Tab. 5.1). The here presented information on the species is limited. More information is available, will be collected and integrated during planned meetings with my cooperation partner in Brazil and will thus inform further analysis of the here presented preliminary approach (cf. section 'Further development of the modelling procedure'). The response variable was the counts of species per forest patch (Pardini et al. 2005). The predictor variables comprised vertical stratification, i.e. terrestrial vs. scansorial, species classification, i.e. marsupials vs. rodents (derived from expert knowledge), patch size of patch *i* ($PS_i$), patch isolation (derived from a GIS map) and matrix intolerance, $MI_s$ (Tab. 5.1, Eq. 5.1). We calculated matrix intolerance from the data of small mammal counts in the matrix (Umetsu and Pardini 2007). The estimate was based on the captured individuals of species *s* (*abundance$_s$*) and the captured individuals of the most abundant species (*abundance$_{max}$*; species numbers were summed up over all sampled matrix habitat types).

$$MI_s = 1 - \frac{abundance_s}{abundance_{max}} \qquad\qquad (5.1)$$

Patch isolation was determined by the minimum edge-to-edge Euclidean distance between patch $i$ and its nearest neighbouring forest patch, $ETE_{min}$. Euclidean distances were calculated using ArcView GIS 3.3 and the extension Nearest Features v3.8b (Jenness 2007).

# 5.3 Modelling approaches

We compared three different models: a mechanistic simulation model with Bayesian parameter calibration (cf. section 'MMB'), a statistical generalized linear model (cf. section 'GLM'), and a null model (cf. section 'Null model').

***Mechanistic simulation model with Bayesian parameter calibration, MMB***

The development of the mechanistic simulation model with Bayesian parameter calibration (MMB) included three steps: First, implementation of a mechanistic and deterministic model that simulates demographic processes of the community to calculate the expected number of individuals per species, $s$, and patch, $i$; second, defining a sampling model, i.e. a relation between these expected occurrences and the likelihood to sample the observed number of individuals; and third, applying a Markov chain Monte Carlo algorithm to estimate parameters of the mechanistic model within a Bayesian framework (Fig. 5.3).

*Overview of processes*

The mechanistic model run on a simplified representation of the study area describing the landscape as a network of forest patches (all 309 patches in the study area that are bigger than 0.5 ha were considered including the 18 patches that were investigated in the field study, cf. Fig. 5.2). Each forest patch $i$ was characterized by patch size, $PS_i$, and minimal edge-to-edge Euclidean distances to all other patches $j$, $ETE_{ij}$, and could potentially be occupied by a subpopulation of each species.

The model calculated the expected local abundances of 18 small mammal species in yearly time-steps. For the total number of simulated years, $TMAX$, a range of 20 to 400 years was considered. We assumed a minimum of 20 years to allow for some development of community dynamics after implementation and a maximum of 400 years as the landscape is

temporally dynamic and species abundances are therefore unlikely to represent long-term adaptations to landscape structure. In each year, subpopulations grew, dispersed and suffered from local disturbances. Density dependent reproduction and mortality was summarized as growth. Patch sizes, species growth rates, intraspecific density regulation and pairwise competition with other species on the patch influenced the growth process. Dispersal was density independent and determined the exchange of individuals between patches. It was influenced by inter-patch distances, species dispersal distances, emigration rates, and dispersal mortality. Additionally, disturbances added a density independent mortality risk.

The model was initialized with local populations of each species that have densities in equilibrium at the scale of the entire landscape, but at least with 0.1 individuals per ha (the model simulated expected values and therefore used positive real numbers). Equilibrium densities for each parameter combination were determined by simulating population growth of all species together on one large patch ($PS$ = 10.000ha) with an initial number of 100 individuals until either 1000 years passed or local population sizes did not change more than 0.1% between consecutive time-steps.

*Detailed description of spatio-temporal community dynamics*

The small mammal species from the Atlantic forest are very similar with regard to size, weight and habitat use. Due to this and the lack of detailed data on differences in life history traits, such as habitat area requirements, dispersal distances and number of offspring, we assumed them to generally equal each other in all traits. Only if any information like data or expert knowledge hinted towards differences between species or species groups we estimated species- or group-specific parameter values (Tab. 5.3).

*Growth* − Local population growth was described by the equation of Maynard Smith and Slatkin (Maynard Smith and Slatkin 1973; Hassell and Comins 1976):

$$N_{i,s}(t+1) = \frac{N_{i,s}(t) \cdot R}{\left(1 + (R-1)\left(\frac{TN_{i,s}(t)}{CC_{i,s}(t)}\right)\right)} \tag{5.2}$$

$N_{i,s}(t)$ is the population size on patch $i$ of species $s$ at time $t$ and $R$ is its maximum growth rate. We estimated two values for $R$, one for marsupials, $R_{mar}$, and one for rodents, $R_{rod}$, and allowed for a broad range of one to ten offspring for possible parameter values of both growth

rates. Species growth was limited by the relation between the local carrying capacity, $CC_i$, and the weighted total number of individuals from all species living on the patch, $TN_{i,s}$. The local carrying capacities depended on patch size, $PS_i$, and species home ranges, $HR$, describing how many hectares were needed per individual: $CC_i = PS_i / HR$. We assumed the home ranges to lie between 0.01ha and 1.5ha.

*Intra-and interspecific competition* – The weighted total number of individuals, $TN_{i,s}$, defined the competition for resources of species $s$ with itself and all other present species:

$$TN_{i,s}(t) = \sum_{p=1}^{18} a N_{i,p}(t) \tag{5.3}$$

The weighting factor $a$ determined the strength of competition between species $p$ and $s$ ($a=0$ corresponded to zero competition and $a=1$ corresponded to interspecific competition being as strong as intraspecific competition because intraspecific competition was set to one). With regard to vertical stratification, we assumed that species sharing the same habitat type competed more strongly than species whose habitats overlapped only partly (Tab. 5.1). Thus, we estimated three values for $a$: one for competition between terrestrial, $a_{tt}$, and scansorial species, $a_{ss}$, respectively, and one for competition of terrestrial with scansorial species or vice versa, $a_{ts}$. Possible values for $a$ ranged between zero and one in each case.

*Dispersal* – After growth, a fraction of the subpopulations determined by the emigration rate, $RE$, emigrated from each patch. We assumed potential emigration rates to range between 0 and 0.5. A matrix of transfer rates, $RT_{ij,s}$, described the fraction of emigrants that moved from patch $i$ to patch $j$. They were calculated by inter-patch connectivity, $PC_{ij}$, and by survival rates during dispersal, $RS_{ij,s}$: $RT_{ij,s} = PC_{ij} \cdot RS_{ij,s}$. Inter-patch connectivity increased exponentially with decreasing minimum inter-patch distance, $ETE_{ij}$, and increasing species' mean dispersal distance, $DD$. We defined potential dispersal distances to range from 0 to 1000 m:

$$PC_{ij,s} = \frac{\exp\left(-\dfrac{ETE_{ij}}{DD}\right)}{\sum_{j} \exp\left(-\dfrac{ETE_{ij}}{DD}\right)} \tag{5.4}$$

Survival, $RS_{ij,s}$, decreased exponentially with increasing species-specific mortality rates, $RM_s$, and inter-patch distances, $ETE_{ij}$, $RS_{ij,s} = e^{-RM_s \cdot ETE_{ij}}$. We assumed mortality rates to depend on species matrix intolerance. We therefore estimated a constant base mortality rate, $BRM$, for all species and multiplied it by the species-specific matrix intolerance, $MI_s$. We set the range of possible values for the base mortality rate to 0 and 1.

**Table 5.2:** Overview of predictor variables (which were assumed to be known), latent variables (which were derived during simulations), and parameters (which were unknown and needed to be calibrated). The subscripts $i$ and j refer to a certain patch, $s$ to a certain species and $t$ to a certain year.

| Symbol | Name | Influenced process | Value or range |
|---|---|---|---|
| *Predictor variables* | | | |
| NS | Number of species | All | 18 |
| $PS_i$ | Patch size | All | [0.5;374] ha |
| $ETE_{ij}$ | Euclidean distance ($ETE_{min}$ is the distance to the nearest neighbour) | Dispersal | [5;14144] m |
| NP | Number of forest patches | Dispersal | 309 |
| $MI_s$ | Matrix intolerance | Dispersal | 0-1 |
| *Latent variables* | | | |
| $N_{i,s}(t)$ | Expected number of individuals | All | |
| $Pred_{i,s}$ | Expected number of sampled individuals | All | |
| $CC_i$ | Carrying capacity | Local growth | |
| $TN_{i,s}$ | Overall competition pressure | Local growth | |
| $RS_{ij,s}$ | Survival during dispersal | Dispersal | |
| $PC_{ij}$ | Inter-patch connectivity (not considering dispersal mortality) | Dispersal | |
| $RT_{ij,s}$ | Transfer rates between patches (considering dispersal mortality) | Dispersal | |
| $RM_s$ | Mortality rate | Dispersal | |
| *Parameters* | | | |
| TMAX | Number of simulated years | All | 20-400 years |
| $R_{mar}$ | Maximum growth rate of marsupials | Local growth | 1-10 offspring per individual |
| $R_{rod}$ | Maximum growth rate of rodents | Local growth | 1-10 offspring per individual |
| HR | Species home ranges | Local growth | 0.01-1.5 ha |
| $a_{tt}$ | Relative strength of competition within terrestrial species | Local growth | 0-1 |
| $a_{ss}$ | Relative strength of competition within scansorial species | Local growth | 0-1 |
| $a_{ts}$ | Relative strength of competition between terrestrial and scansorial species | Local growth | 0-1 |
| RE | Emigration rate | Dispersal | 0-0.5 |
| DD | Mean dispersal distance | Dispersal | 0-1000 m |
| BRM | Base mortality rate | Dispersal | 0-0.2 |
| ND | Number of individuals dieing during an disturbance event | Disturbances | 0-0.6 individuals |
| TD | Time interval of disturbances | Disturbances | 1-20 years |

*Disturbances* – We assumed disturbances to be important because most of the forest remnants in our study area were privately owned (Myers et al. 2000), their local state was highly dependent on farmers' attitudes and thus prone to frequent disturbances (Pardini 2004). Small patches particularly sufferd as edge effects and disturbances from outside the patch were strong (Barbosa and Marquet 2002; Taylor et al. 2001). In the model, disturbances occurred independently on each patch and for each species after a time interval of *TD* years. At each disturbance event an absolute number of *ND* individuals died. Both the intensity of disturbances and the frequency of disturbances were equal for all species and patches. We defined potential values for disturbance intensity to range from 0 to 0.6 dying individuals per patch (with the number of surviving individuals always greater than or equal to zero) and for disturbance frequency to range from every to every 20$^{th}$ year. Disturbances never occurred in the first and in the last two years to avoid too strong influence on model output.

*Sampling model*

The sampling model related the calculated abundances of species *s* in patch *i* to the predicted number of captured individuals of the same species in the same patch, *Pred*$_{i,s}$. We suggested the expected numbers of individuals per ha to correspond directly to *Pred*$_{i,s}$. As capture numbers were count data, we assumed them to follow a Poisson distribution:

$$Pred_{i,s} = \frac{N_{i,s}(t = TMAX)}{PS_i} \tag{5.5}$$

*Bayesian parameter calibration*

The mechanistic and sampling models were based on the 12-dimensional parameter vector, $\theta$, and the five-dimensional vector of predictor variables, *x* (Tab. 5.2). Regarding growth, dispersal, disturbance and sampling processes the model calculated latent variables, such as carrying capacities and predicted capture numbers. The predicted capture numbers could then be compared with the vector of observed capture numbers, *y* (Fig. 5.3). In its simplest form, our model can be formalized as follows:

$$p(\theta/y, x) \propto p(y/\theta, x) \cdot p(\theta) \tag{5.6}$$

where $p()$ represents a distribution or density. On the left hand side is the posterior distribution of parameters, on the right hand site the likelihood, $p(y/\theta, x)$, and the prior distribution of parameters, $p(\theta)$. There is no distribution for $x$, because the predictor variables were assumed to be known (sampled without error). We suggested prior distributions of the parameters to be flat, independent of each other and with boundaries based on expert and literature knowledge (cf. section 'Model description'). Following the sampling model the likelihood was defined as:

$$p(y/\theta, x) = \prod_{i=1}^{18} \prod_{s=1}^{18} dPois(y_{i,s}, Pred_{i,s})$$

(5.7)

where $dPois(z, mu)$ is the density of the Poisson distribution at point $z$ with mean $mu$.
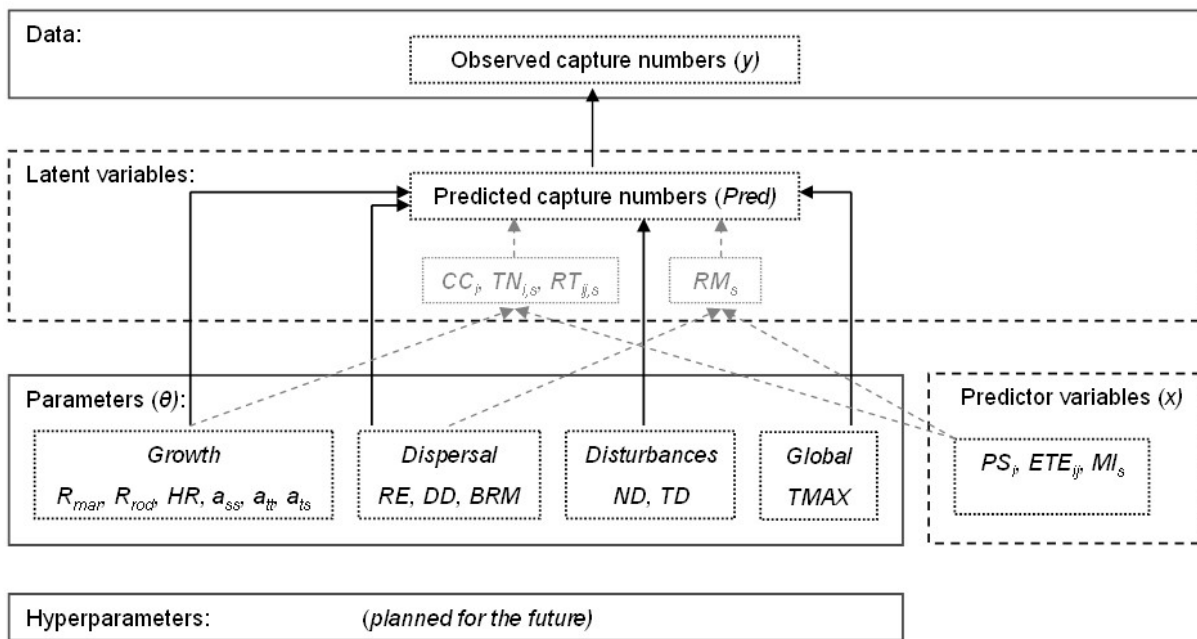


**Figure 5.3:** Schematic overview of the full mechanistic model, showing observed abundances in the upper data stage, variables derived during simulations in the latent variables stage and unknowns with assigned prior distributions in the parameters (and hyperparameters) stage. Parameters of the three processes growth, dispersal, and disturbances together with predictor variables parameterized the mechanistic model. The output of this model is a prediction of numbers of captured individuals which can be related to the field data. Stages with solid lines belong to the Bayes model structure: Parameters and data define a simple Bayesian model; acknowledging the variability in parameters would necessitate a hyperparameter stage and thus would result in a hierarchical Bayes model (not included in this chapter).

We used the Metropolis-Hastings algorithm to estimate the posterior distribution of the parameters because an analytical solution was not possible. The Metropolis-Hastings algorithm is a Markov Chain Monte Carlo (MCMC) sampling algorithm which creates a sequence of samples from a given multi-dimensional distribution (Metropolis et al. 1953; Robert and Casella 1999). MCMC algorithms are used to create a 'shape' of a distribution when the latter can be calculated at each point, but the multi-dimensional shape is unknown. The sequence of samples converges to the input distribution as the Markov chain reaches its stationary distribution. A random set of values from the parameters' prior distributions can be used as a starting point, $\theta_1$, for the algorithm. In a next step, a proposal for a new set of values, $\theta`$, based on the existing values at step $n$, $\theta_n$, is generated: $\theta' = \theta_n + \varepsilon$, where $\varepsilon$ is a random vector with $p(\varepsilon) = p(-\varepsilon)$. The variance of the distribution of $\varepsilon$ determines the step-length of the algorithm. Acceptance of the proposal for $\theta$ as the new value $\theta_{n+1}$ depends on the ratio

$$\beta = \frac{p(\theta'/y)}{p(\theta_n/y)} = \frac{p(y/\theta') \cdot p(\theta')}{p(y/\theta_n) \cdot p(\theta_n)} \qquad (5.8)$$

If $\beta$ is greater or equal to one, $\theta'$ is always accepted. If $\beta$ is smaller than one, $\theta'$ is accepted with probability $\beta$. Thereby, in the likelihood landscape the algorithm always accepts a proposal which points 'uphill'. A proposal that points 'downhill' is accepted with a probability equivalent to the ratio of absolute elevations in the likelihood landscape. We implemented the algorithm with reflecting boundaries (at the boundaries of the flat prior distributions).

We run 16 chains of the Metropolis-Hastings sampling algorithm. Step-lengths between accepted and newly proposed parameter vectors were normally distributed with mean of zero and with variances equal to the square of 0.5% of the prior parameter ranges. Acceptance rates were low and ranged between 0.001 and 0.182. The first 20,000 steps of each chain were defined as 'burn-in' and were not considered in the further analysis (Gilks et al. 1996). To reduce the amount of data, chains were thinned out by taking only every 50th step. The resulting posterior distribution is described by 10,489 data points.

### Statistical generalized linear model (GLM)

The maximal model we considered predicted main and two-way interaction effects of species characteristics (habitat use, classification, and matrix intolerance) and landscape characteristics (patch size and minimal distance to the nearest neighbour) on small mammal abundances assuming a Poisson error distribution for the counts. We transformed the explanatory variables considering 'first aid transformations' (Mosteller and Tukey 1977). We took logarithms of patch size as well as minimal distance and arcsine-transformed matrix intolerance. Starting with the maximal model we performed stepwise backward selection based on the Akaike information criterion (AIC, R-function step, Venables and Ripley 2002). The residuals of the selected most parsimonious model showed no critical derivations from the assumptions of generalized linear models. However, p-values were not exact as the model does not include species interactions, and these interaction effects therefore are contained in the error terms.

### Null model

The null model predicted the overall mean of captures in the field data over all species and all patches for each data point.

### Model comparison

We compared the different models with regard to log-likelihood (*logLik*), Akaike's information criterion and a pseudo R-square measure. Our pseudo R-square measure definition based on deviances: $R^2 = 1 - D(resid)/D(null)$, where *D(resid)* and *D(null)* denote the residual deviance, *2logLik(max)-2logLik(fitted)*, and the null deviance, *2logLik(max)-2logLik(null)*, of the model in focus, respectively (Waldhör et al. 1998). The log-likelihoods *logLik(max)*, *logLik(fitted)* and *logLik(null)* denoted the maximal log-likelihood, the log-likelihood of the model in focus and the log-likelihood of the null model, respectively. If not stated differently, analyses of the mechanistic model refered to the means of 100 random simulations from the posterior distribution.

We calculated biodiversity within and among patches. The number of species per patch defined alpha diversity. We determined beta and gamma diversity in each case within a reference group of patches with similar size. To find these reference groups, we ordered patches by size and then compared each patch with its two smaller and two bigger neighbours. We calculated beta diversity for all pairs of patches in a reference group and took the mean to

obtain a single value per patch. As a metric we used *min(b, c)/[min(b, c) + a]*, where *a* is the total number of species which are found in both patches, *b* is the number of species which are present in the other patch but not in the focal patch and *c* is the number present in the focal patch but not in the other patch (Lennon et al. 2001). For each reference group, we determined gamma diversity by the total number of species.

The mechanistic simulation model with Bayesian parameter calibration was implemented with the Borland C++ Builder 5 using numerical routines from the GNU Scientific Library (http://sources.redhat.com/gsl/ref/gsl-ref_toc.html) for the probability distributions, and graphics and statistics were generated in R 2.6.1 (R Development Core Team 2007).

## 5.4 Results

Below, we first present the current state of the parameterisation of the mechanistic simulation model (cf. section 'Preliminary results'). Secondly, we quantitatively compare model fits (cf. section 'Model evaluation') and analyse parameter estimates for the mechanistic (cf. section 'Parameter estimation for MMB') and the regression model (cf. section 'Parameter estimation for GLM'). Then, we investigate the development of population dynamics over time in different patches with the mechanistic model (cf. section 'Spatio-temporal population dynamics'). Finally, we qualitatively analyse emerging diversity patterns at local and regional scales with the mechanistic model and broaden the spatial focus by examining these patterns for more patches (not only for the 18 patches from the field study) and over longer time periods (cf. section 'Diversity patterns across scales').

### *Preliminary results*

At the current state of analysis, the MCMC algorithm has not fully converged. As a temporary convergence criterion we used the fact that the posterior distribution of a neutral parameter, i.e. a parameter that passes through the MCMC algorithm but has no influence on the mechanistic model, should equal the prior distribution. This criterion is clearly not fulfilled after six weeks of simulation (Fig. 5.4), indicating that the used MCMC algorithm has not reached equilibrium and is too time-inefficient for the question. Therefore, the following results from the mechanistic simulation model with Bayesian parameter calibration should be treated as preliminary.
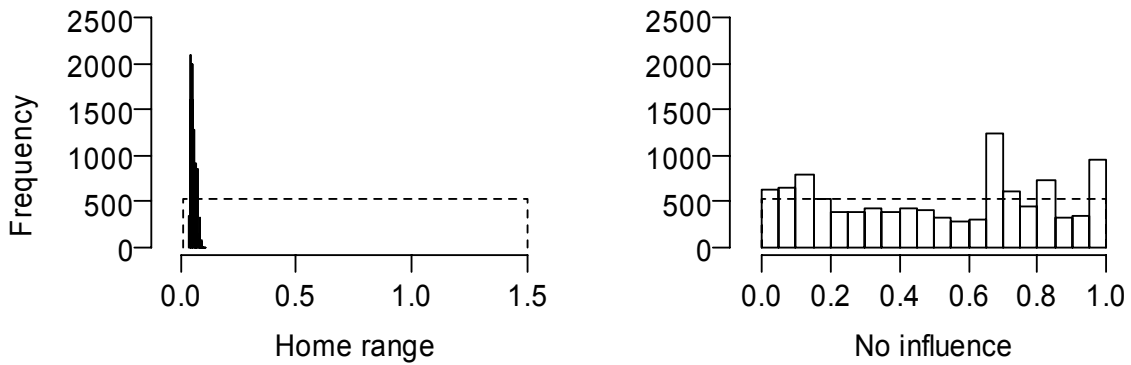
**Figure 5.4:** Prior (dashed) and posterior (solid) distributions of a model parameter (home range, left) and a neutral parameter, i.e. a parameter defined to have no influence on the mechanistic model (right). After convergence, the posterior distribution of the un-informative parameter should equal its prior distribution, a criterion not completely fulfilled yet.

### *Model evaluation*

We found that the best mechanistic model (best MMB) performs much better than a null model (Tab. 5.3). The pseudo R-square value indicates that 25% of the variation in the data is explained by the best MMB.

**Table 5.3:** Fit indices for the null model, the best mechanistic model (MMB with highest likelihood), and the regression model (GLM).

|  | Null model | MMB (best fit) | GLM |
|---|---|---|---|
| *LogLik* | -859 | -704 | - 639 |
| *AIC* | 1721 | 1432 | 1307 |
| *Pseudo R-square* | 0 | 0.25 | 0.36 |

The regression model (GLM) performs better than the best MMB with regard to likelihood, pseudo R-square, and the Akaike information criterion (AIC, Tab. 5.3). Both the GLM and the MMB have problems to predict very high observed densities (Fig. 5.5). The MMB additionally overestimates predictions at low observed densities more strongly (Fig. 5.5). Generally, the performances of the mechanistic model and the regression model are relatively similar when compared to the poor performance of the null model (Tab. 5.3).
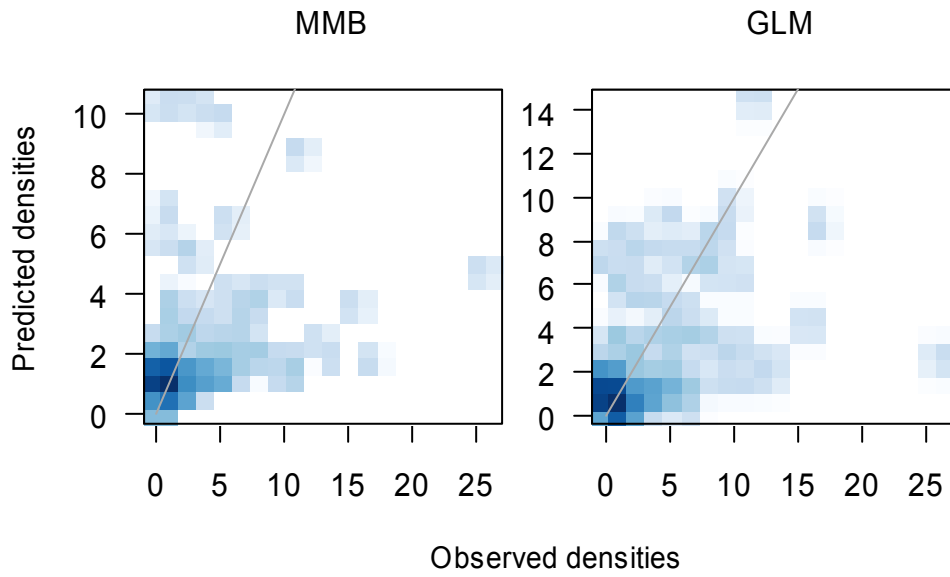
**Figure 5.5:** Predicted species densities against observed species densities for the mechanistic model (MMB) and the regression model (GLM). The darker the colour the more often this area of the plot is realised. The grey line indicates where predictions would exactly match observations.
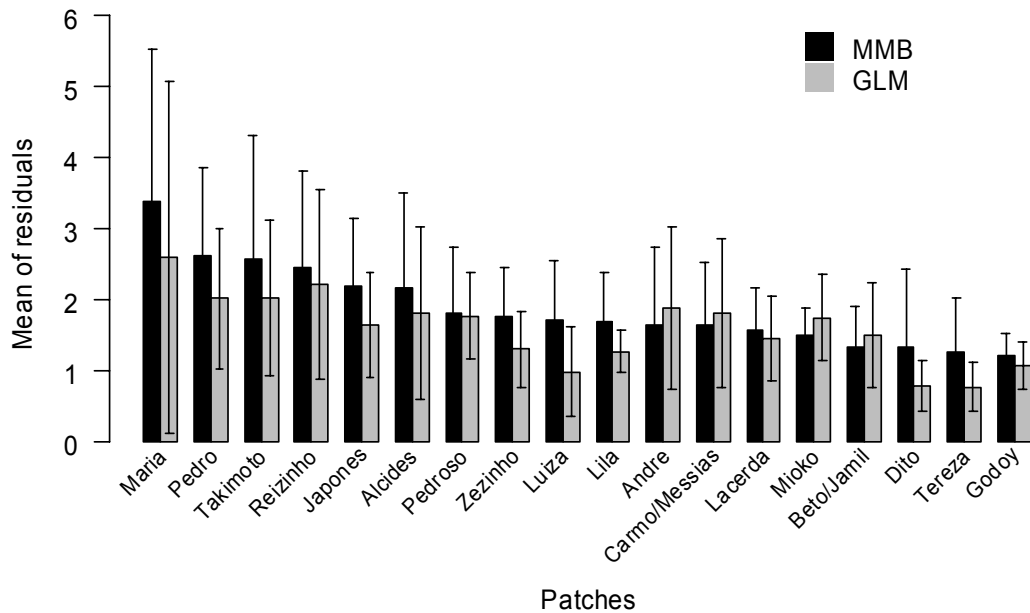


**Figure 5.6:** Mean of residuals summed over all species for all 18 patches for the mechanistic model (MMB, black) and the regression model (GLM, grey) with 95% confidence interval (mean +/- 1.96 times the standard error).

The means of residuals per patch, i.e. the deviations of predicted values from observed values summed over all species, are mostly higher for the mechanistic model than for the regression model (Fig. 5.6). Only for a few patches the mechanistic model outperforms the regression model (e.g., for 'Andre' and 'Mloko').

### *Parameter estimation for MMB*

The estimates of model parameters inform about the influence and the relevance of correlates, process parameters and corresponding processes for the small mammal community structure. Mean estimates describe the processes, and parameter uncertainties are related to the relevance of the parameters, with very large uncertainties indicating low relevance.

For the mechanistic model the MCMC algorithm produced a 12-dimensional cloud of points, each being a plausible parameter combination. In some regions of the cloud the points occur more densely, indicating that parameter values in these regions have a higher posterior probability than those in the sparser regions.

Plotting the univariate histograms of the parameters, we found broad ranges of probable values for some parameters but narrow ones for others (Fig. 5.7). Especially species' home ranges, dispersal mortality (influenced by species specific intolerance to cross the matrix), disturbance frequency and intensity, competition and dispersal parameters seem to be restricted. Parameter calibration suggests low home ranges (< 0.2ha), high disturbance frequency (mostly more than every fourth year) with strong disturbance intensity (> 0.4 dying individuals per ha), strong interspecific competition within the groups of terrestrial and scansorial species (mostly > 0.5) and lower competition between these groups (mostly > 0.1), small dispersal distances (< 150m), low or moderate emigration rates (between 0 and 0.3), and zero or moderate mean dispersal mortality (0 or 0.02-0.03).

We calculated the matrix of Pearson correlation coefficients to determine the correlation structure of the posterior distribution. Four coefficients exceed 0.7 (Tab. 5.4). Reproduction rates of marsupials and rodents as well as interspecific competition within scansorials and within terrestrials are the most strongly correlated parameters. Furthermore, competition within scansorials and competition within terrestrials correlate strongly with the total number of simulated years.
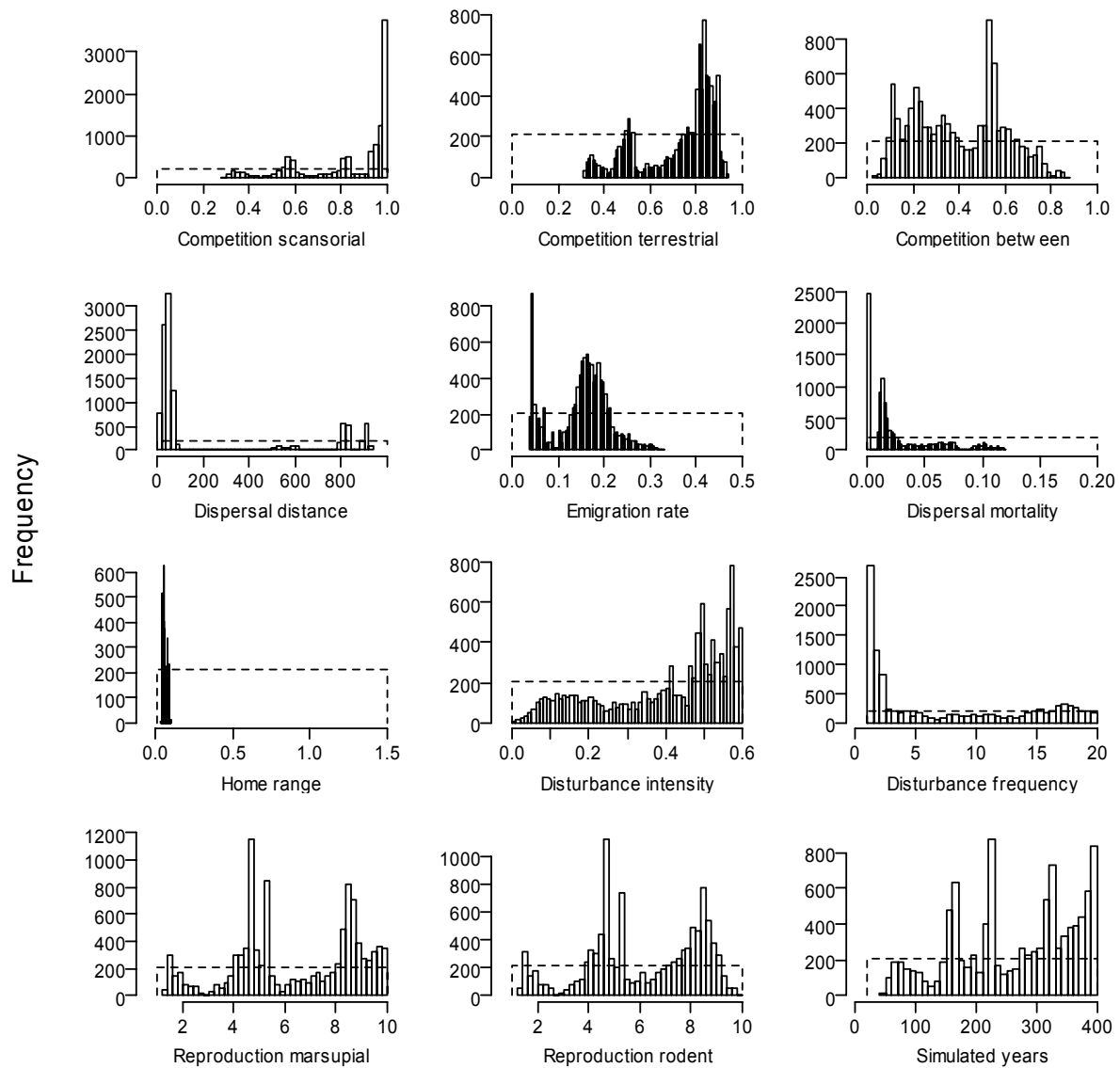
**Figure 5.7:** Prior (dashed) and posterior (solid) distributions of the MMB model parameters. The upper panel reveals very strong interspecific competition within terrestrial and scansorial species groups and reduced competition between these groups. The second panel of dispersal parameters, with low mean dispersal distances, low emigration rates and low dispersal mortality, shows that species are able to disperse between patches but that exchange is not very frequent.

At this stage of analysis, the specified model structure allows for species differences in interspecific competition, in dispersal mortality (because it depends on species specific matrix intolerance) and in reproduction rates. Parameter estimation suggests species to strongly differ in interspecific competition and to moderately differ in dispersal mortality (for all values

greater than zero) while reproduction rates are suggested to be very similar for rodents and marsupials. In the next planned step of analysis, hyperparameters will be integrated and will allow for more flexibility with regard to species differences (cf. section 'Further development of the modelling procedure').

**Table 5.4:** Parameters with correlations among posterior distributions greater than 0.7

| Parameter | Parameter | Correlation coefficient |
|---|---|---|
| *Reproduction rates of marsupials* | *Reproduction rates of rodents* | 0.99 |
| *Intersp. competition within scansorials* | *Intersp. competition within terrestrials* | 0.91 |
| *Intersp. competition within scansorials* | *Number of simulated years* | 0.75 |
| *Intersp. competition within terrestrials* | *Number of simulated years* | 0.75 |

## *Parameter estimation for GLM*

The parameterization of the regression model identifies species specific matrix intolerance (z=-11.9, p<0.01, Tab. 5.5) and species classification (z=-5.4, p<0.01) as the most influential variables (only the first result is congruent with results from the MMB).

**Table 5.5:** Minimal adequate model for species abundances (maximal model included all main effects and two-way interactions between area, $PS_i$, isolation, $ETE_{ij}$, species classification, species habitat use and species matrix intolerance, $MI_s$; Null deviance: 1332 on 323 degrees of freedom, residual deviance: 889 on 310 degrees of freedom)

| Parameter | Estimate | Std. error | z-value | p-value | Level |
|---|---|---|---|---|---|
| (Intercept) | 30.87 | 2.58 | 11.96 | < 0.001 | *** |
| $\log(PS_i)$ | -0.26 | 0.15 | -1.74 | 0.082 | |
| $\log(ETE_{min})$ | -0.55 | 0.23 | -2.41 | 0.016 | * |
| Habitat use (terrestrial) | -8.20 | 2.96 | -2.77 | 0.006 | ** |
| Classification (rodent) | -19.57 | 3.59 | -5.45 | < 0.001 | *** |
| $asin(sqrt(MI_s))$ | -19.98 | 1.68 | -11.88 | < 0.001 | *** |
| $\log(PS_i)$ x $\log(ETE_{min})$ | 0.14 | 0.04 | 3.19 | 0.001 | ** |
| $\log(PS_i)$ * Classification (rodent) | -0.14 | 0.09 | -1.61 | 0.107 | |
| $\log(PS_i)$ * $asin(sqrt(MI_s))$ | 0.12 | 0.06 | 1.97 | 0.049 | * |
| $\log(ETE_{min})$ * Classification (rodent) | 0.33 | 0.13 | -2.45 | 0.014 | * |
| $\log(ETE_{min})$ * $asin(sqrt(MI_s))$ | 0.19 | 0.11 | 1.72 | 0.085 | |
| Habitat use (terrestrial) * Classification (rodent) | 1.31 | 0.48 | 2.75 | 0.006 | ** |
| Habitat use (terrestrial) * $asin(sqrt(MI_s))$ | 5.16 | 1.88 | 2.74 | 0.006 | ** |
| Classification (rodent) * $asin(sqrt(MI_s))$ | 12.83 | 2.48 | 5.17 | < 0.001 | *** |

Significance levels: * < 0.05, ** < 0.01 and *** < 0.001; First-aid-transformations: log = natural-logarithm, asin = arcsine, sqrt = square-root

The less often species are captured in the matrix (cf. data by Umetsu and Pardini 2007) the less abundant they are in the patches. Rodents are generally less abundant than marsupials, and matrix intolerant marsupials are more vulnerable than matrix intolerant rodents (z=5.2, p<0.01). Main effects of patch isolation and patch size are relatively unimportant. However, their interaction has a strong positive effect on abundances (z=3.2, p<0.01) indicating that small patches suffer from strong isolation.

### *Spatio-temporal population dynamics resulting from the MMB*

The spatially explicit community dynamics in the parameterized mechanistic model show a clear dependency on patch size. In small patches a number of species goes extinct and patches are typically dominated by a few frequent species (Fig. 5.8, left column). In isolated small patches one or two species suppress or even displace all other species while in less isolated small patches species diversity is a bit higher.

In larger patches, time to extinction is higher and most species are able to survive at least up to 300 years (Fig. 5.8, right column). The most abundant species is less dominant than in small patches and in most cases a higher number of frequent species occur. Differences between isolated and well-connected patches are less important in larger patches than in smaller ones.

Decreasing disturbance frequency increases the dominance of the most abundant species and reduces species diversity within large patches but tends to increase species diversity within small patches (Fig. 5.8, upper four plots vs. lower four plots).
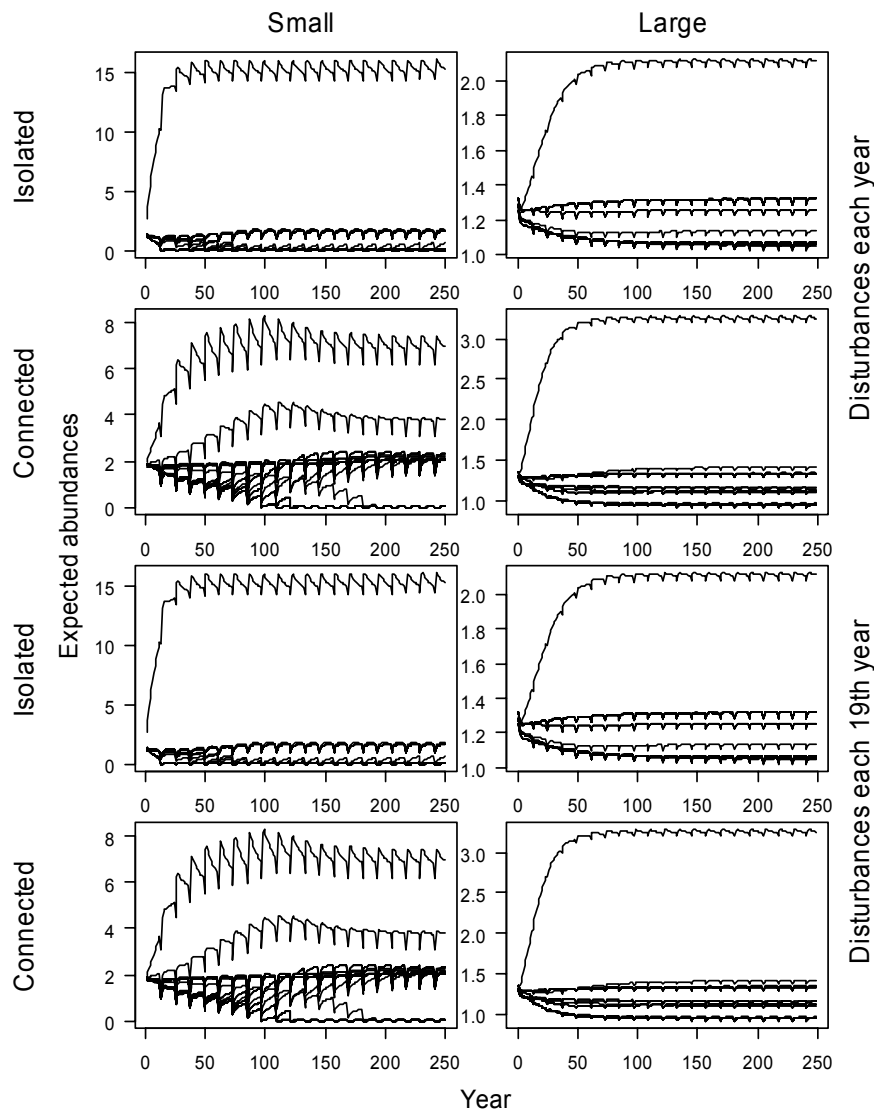
**Figure 5.8:** Expected abundances of species over time with disturbances every year (upper four plots represent abundances in four different patches in a simulation with specific parameter values) and with disturbances every 19th year (lower four plots represent abundances in the same four patches but in another simulation with different parameter values). For each disturbance regime, the following four patches are compared: a small and isolated patch (10ha and 103m minimum distance to a neighbouring patch), a large and isolated patch (19ha and 95m minimum distance to a neighbouring patch), a small and well connected patch (9ha and 5m minimum distance to a neighbouring patch) and a large and well connected patch (18ha and 5m minimum distance to a neighbouring patch). The different lines represent the 18 different species interacting in the community.
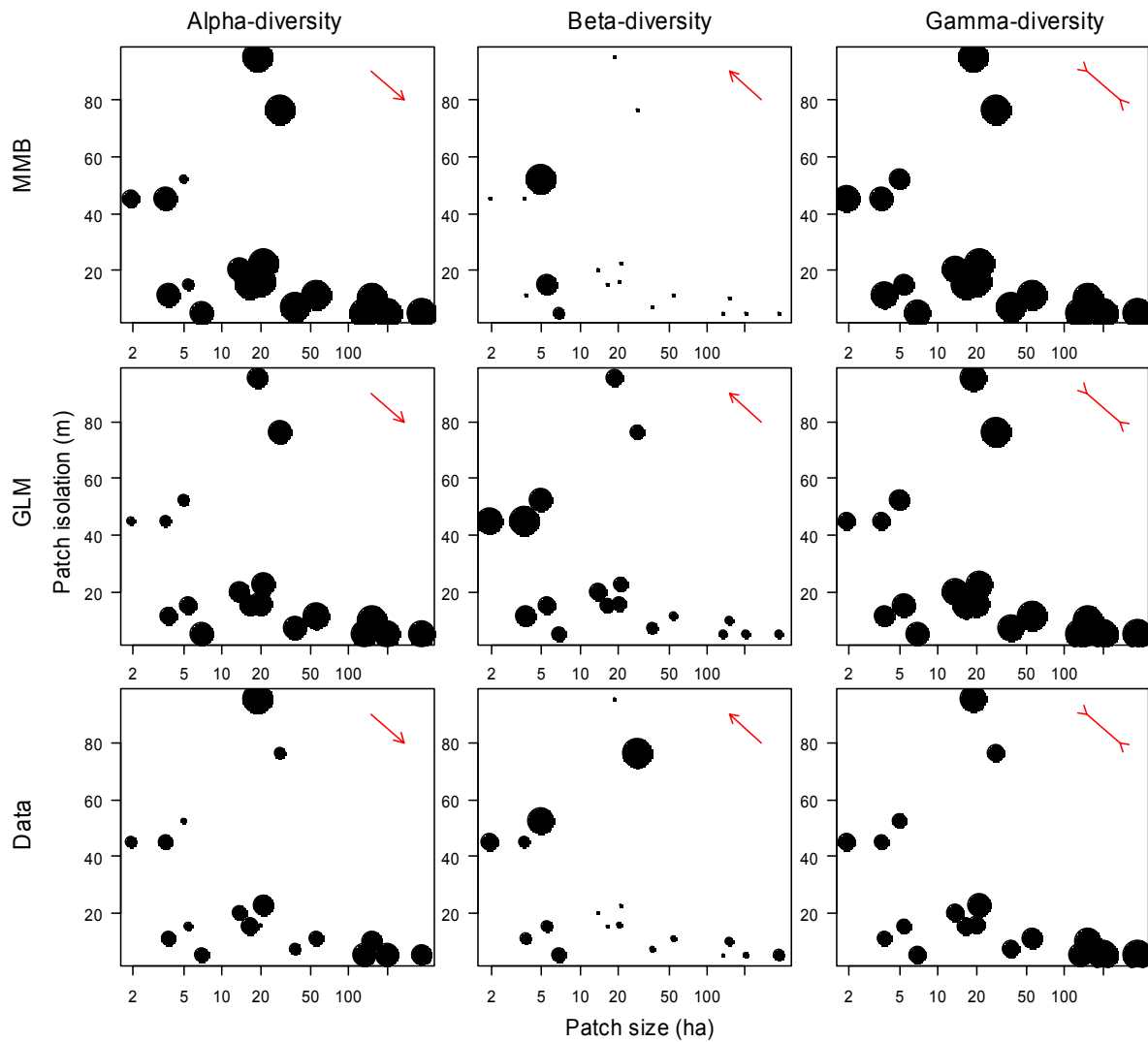
**Figure 5.9:** Species diversity on different scales in relation to patch size and patch isolation (nearest neighbour distance) for the mechanistic model (MMB), the regression model (GLM) and the data; we regard diversity within patches (alpha-diversity), between patches of similar size (beta diversity) and among patches of similar size (gamma diversity); the larger the circles the higher the values of the diversity indices; red arrows indicate the direction of the hypothesized relation: Alpha diversity increases and beta diversity decreases for larger and less isolated patches, whereas gamma diversity is not influenced by patch size and isolation.

### *Diversity patterns across scales*

Qualitatively analysing the relation of diversity on different scales with patch size and patch isolation, we found for the 18 patches analysed in the field study a general pattern that the data share with predictions from both the mechanistic and the regression model (Fig. 5.9): Decreasing size and connectivity of forest patches decreases species diversity within patches

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(alpha-diversity), increases diversity between patches of similar size (beta diversity) and does not influence regional diversity among patches of similar size (gamma diversity). For the data, alpha diversity ranges between 3 and 11, beta diversity ranges between 0.03 and 0.46 and alpha diversity ranges between 7.75 and 12. Diversity indices change over the same range of values for increasing patch sizes and patch isolation in the mechanistic model and the regression model, but changes in the mechanistic model occur more abruptly.
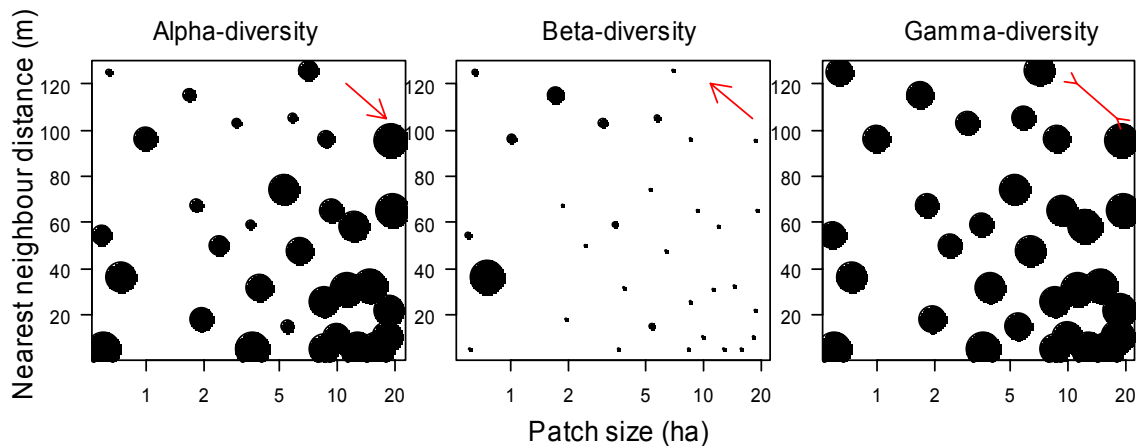


**Figure 5.10:** Species diversity on different scales for patches in the landscape not already analysed in the field study in relation to patch size and patch isolation (nearest neighbour distance) for the mechanistic model (MMB); we regard diversity within patches (alpha-diversity), between patches of similar size (beta diversity) and among patches of similar size (gamma diversity); the larger the circles the higher the values of the diversity indices; red arrows indicate the direction of the hypothesized relation: Alpha diversity increases and beta diversity decreases for larger and less isolated patches, whereas gamma diversity is not influenced by patch size and isolation.

Based on the parameterized MMB, we investigated the diversity pattern of patches in the study landscape not already analysed in the field study (spatial extrapolation of the MMB). We used a range of patch size, $PS_i$, and patch isolation, $ETE_{ij}$, such that combinations were more or less evenly distributed over the parameter space (very large patch sizes were not plotted as they are always combined with low patch isolation). Results show that the general biodiversity pattern already identified in the field data (Fig. 5.9) can be generalized to all patches in the landscape: Decreasing size and increasing isolation of forest patches decreases alpha-diversity, increases beta diversity and does not influence gamma diversity (Fig. 5.10).
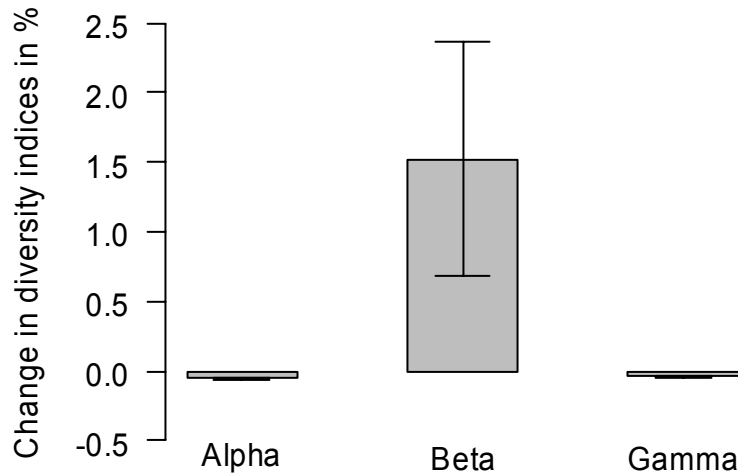
**Figure 5.11:** Percental changes in mean diversity indices between the predicted current community pattern and the predicted community pattern in 200 years with 95% confidence interval (mean Percental changes +/- 1.96 times the standard error).

For long-term predictions of the MMB, we ran 100 simulations with parameterizations from the posterior distribution but increased the simulation time by 200 years and then calculated percental changes in the diversity indices (temporal extrapolation of the model). We found that the mechanistic model, with a constant fragmentation pattern set to the current situation, predicts increasing beta diversity and slightly decreasing alpha and gamma diversity (Fig. 5.11).

## 5.5 Discussion

A better understanding of the mechanisms and processes involved in structuring diverse communities and in governing their response to landscape changes is a major goal of ecologists today. Revealing the relative importance of different types of competitive interactions is one of the pertaining challenges. Here, we combined mechanistic modelling of the intra- and interspecific processes in a small mammal community in the Atlantic Brazilian rainforest (Pardini et al. 2005; Umetsu and Pardini 2007) with recent advances in Bayesian statistics (Van Oijen et al. 2005). We found that both neutral and niche-based coexistence

mechanisms are crucial for community dynamics. Which mechanism dominates a specific interaction depends on the species similarity in their habitat use. Interactions of species that share the same level of vertical forest structure are mostly neutral while interactions of species that differ in their use of vertical forest structure are strongly regulated by niche-based processes.

In our analyses we confronted a mechanistic simulation model and a statistical 'black-box' regression model with field data and compared model fits to evaluate the performance of the mechanistic model. In theory, mechanistic simulation models should outperform regression models with regard to process understanding and generalization as they are able to integrate knowledge about processes acting at different levels of organization, from individuals to populations and communities (Grimm and Railsback 2005). However, parameterization of mechanistic models compared to regression models bares considerable difficulties. Recent advances in Bayesian statistics promise a coherent framework for confronting mechanistic simulation models with data (Van Oijen et al. 2005) but the need for time-efficient algorithms to determine posterior distributions of parameter values makes the task challenging (Tierney 1994; Haario et al. 2006). In our approach, we parameterized the mechanistic simulation model with a Metropolis-Hastings algorithm (Metropolis et al. 1953; Robert and Casella 1999). So far, this algorithm has proved to be too time-inefficient for the question, and thus the results presented here must be taken as preliminary.

Comparing the results from the mechanistic and the regression model with field data, we found that both models outperform the null model. The regression model predicts the data somewhat better than the mechanistic model. However, an improved model calibration (cf. section 'Further development of the modelling procedure') could reduce or even reverse this performance difference. Most notably, our approach of combining a mechanistic simulation model with Bayesian calibration has advantages over a regression model with regard to process understanding and spatio-temporal extrapolation of results.

Results from our modelling procedure suggest that the small mammal community dynamics is governed by both neutral and niche-based influences in a characteristic pattern: Coexistence of species using the same forest layer (terrestrial vs. scansorial) is governed by neutral processes while coexistence of species using different forest layers is dominated by niche differentiation processes. The strongest argument for this hypothesized pattern is provided by the estimates of competition strengths (cf. Fig. 5.7). Both competition strength within terrestrial species and competition strength within scansorial species are close to

intraspecific competition strength, suggesting that fitness-related differences between species are very small and that neutral processes are likley to govern the interactions within these groups. By comparison, competition strength between scansorial and terrestrial species is much lower indicating that species are able to reduce competition strength between groups by a differentiation in fitness-relevant traits.

The assumption of neutral coexistence within scansorial and terrestrial species groups is further supported by (1) the temporal population dynamics and (2) the spatial diversity patterns:

(1) Comparing species abundance dynamics on small isolated patches with dynamics on large and well connected patches (cf. Fig. 5.8), we found that species diversity on small isolated patches decreases faster with time and after a few years only few species dominate the community. The reason is that competition pressure and thus competitive exclusion is increased by the small amount of available resources. Large edge effects, i.e. higher extinction risks because of changing micro-climatic conditions (Barbosa and Marquet 2002; Taylor et al. 2001) and larger pressure from predators (Lahti 2001) further decrease resource availability and thus increase competitive exclusion on small patches. Moreover, the nearest neighbor patch is far and species dispersal distances are restricted such that almost no immigrants reach the patches to substitute the loss of species (Bell 2000; Hubbell 2001; Adler et al. 2007). Only if immigration rates are high, such as in more strongly connected patches, or if extinction rates are low, such as in larger patches, competitive exclusion is slowed down and allowes neutral dynamics to increase the local diversity of the community.

(2) Analyzing diversity patterns on different spatial scales, we found that increasing landscape fragmentation (decreasing size and increasing isolation of forest patches) decreases species diversity within patches, increases diversity between patches and does not influence regional diversity. Local diversity decreases due to the accelerated drift to competitive exclusion in small patches described above. Which species prevail in a patch is at least partly determined by stochasticity because species have similar fitness, leading to high between-patch diversity. Thus, the observed biodiversity patterns are mainly driven by neutral processes with increasing inter-patch diversity balancing the decreasing intra-patch diversity, such that regional diversity stays constant overall.

In addition to the differences in competition strength among pairs of species, differences in fitness-related species traits would support the assumption of niche differentiation influencing competitive interactions (Lotka 1925; Volterra 1926; Gause 1934). We found

species differences in matrix intolerance to be important for species abundances in both the mechanistic (implemented via dispersal mortality) and the regression model but differences in matrix intolerance are small overall. Differences between marsupials and rodents are important in the regression model but not in the mechanistic model (implemented via different reproduction rate parameters). Overall, differences in competition within terrestrial and scansorial species and among these groups clearly hint towards niche differentiation between terrestrial and scansorial species. In contrast, we could not find such clear indications for niche differentiation for marsupials vs. rodents or matrix tolerant vs. matrix intolerant species, respectively. However, the current structure of the simulation model is very restrictive with regard to species differences in parameter estimates and thus implicitly hampers the detection of niche differentiation. An expansion towards a hierarchical model with species-specific parameter estimates would allow for analysing niche differentiation more profoundly (cf. section 'Further development of the modelling procedure').

We found that both neutral and niche-based processes contribute to the dynamics in the small mammal community. These results are in agreement with Adler's (2007) suggestion that in many communities both processes complement each other with gradual transitions where either niche-based coexistence overcomes large fitness differences, or weak niche differentiation is coupled with similar fitness between species. Small mammals are of intermediate size with respect to the rule of thumb of Gotelli and Rohde (2002) that presence-absence patterns for small-bodied taxa with low vagility and/or small populations are mostly random, whereas those for large bodied taxa with high vagility and/or large populations are highly structured.

Our results provide a basis to investigate the fate of the small mammal community on larger scales and to estimate future developments depending on landscape changes. Initial steps we have taken in this direction suggest that regional diversity will not be reduced further if the current landscape fragmentation pattern remains constant but that very different species will occur in different patches and that spatial heterogeneity in the community will increase.

In our rapidly changing landscapes, ecologists often need answers for management questions in time frames that do not allow for the collection of additional ecological data. Understanding the nature of the ecological processes that govern community dynamics and structure is vital for conservation management but is often hampered by limited knowledge and data. We propose the combined approach of a mechanistic simulation model and

Bayesian statistics as a coherent and efficient framework to complement single-species approaches with community-level analysis.

## 5.6 Further development of the modelling procedure

In the future, we aim to improve the preliminary analysis presented here in four steps:

(1) We will implement a more efficient algorithm and use the Gelman-criterion (Gelman and Rubin 1992) to test for convergence. Possible candidates for the improved algorithm are a hybrid of the Gibbs sampler and the Metropolis algorithm (Tierney 1994; Carlin and Louis 2000; Condit et al. 2006) and the DRAM sampler, i.e. a combination of delayed rejection and an adaptive Metropolis sampler (Haario et al. 2006). With these improved techniques we expect the MCMC sampler to converge faster.

(2) We will broaden the approach to a hierarchical Bayesian model. At the moment, species in the model are set to be equal with respect to home ranges, reproduction (except for differences between marsupials and rodents), dispersal distances, emigration rates and disturbance sensitivity. The improvement of the hierarchical approach is to estimate species specific parameter values but to restrict these values by assuming them to belong to a common distribution, the hyperdistribution defined by the hyperparameters (indicated in Fig. 5.3). This change in parameterization will result in a more realistic and more flexible model (Carlin et al. 2006). We would expect the hierarchical approach to enhance estimation accuracy and model fit while, at the same time, preventing over-fitting.

(3) For the region of Caucaia a new dataset with capture data from a subsequent year has become available very recently. This information will be used for updating the parameter calibration, which will decrease model uncertainty.

(4) Currently used prior distributions are relatively uninformative. However, better data and more accurate expert knowledge are available and will be the subject of further discussions with our cooperation partners in São Paulo. These discussions will inform the model and the prior distributions, and will thus help to improve estimation accuracy.

# Synthesis

This final chapter has three parts. First, I summarize the key findings of this thesis and their ecological implications. Second, I discuss the significance of the results with regard to both the scientific gain of knowledge and the utility for species conservation. Finally, I suggest areas for potential and planned further research.

## Pieces of a whole

The general question addressed in this thesis was to increase our predictive understanding of the response of populations and communities to climate change and habitat fragmentation. The main finding with regard to this question is that density regulation, as it emerges from both interspecific and intraspecific competitive interactions within the communities, strongly modifies and sometimes completely reverses the response to environmental change. The thesis reveals that density regulation influences not only species persistence but also coexistence and might even expose new phenomena, such as coexistence through over-compensation.

Although each chapter of this thesis represents an independent study and in this sense is autonomous, taken together they provide a broader picture, highlighting that understanding the nature of competitive interactions has considerable potential for explaining species coexistence and predicting and managing population- to community-level consequences of environmental change for biodiversity.

Species living in fragmented landscapes persist regionally if recolonization counteracts local extinction. The over-compensation of local densities accelerates the extinction of sub-populations by generating strong and deterministic density fluctuations that add to the threat of demographic and environmental stochasticity. In this thesis, I have shown that considering density regulation another process becomes important: the synchronizing effect of dispersal and the resulting spatial synchrony of sub-population dynamics. Strongly synchronized dynamics result in a simultaneous local decline and thus in a regional extinction (e.g. Hanski 1991). As strong dispersal enhances spatial synchrony, dispersal needs to be well balanced: It

has to be strong enough to ensure sufficient recolonization but weak enough to prevent spatial synchrony (Münkemüller and Johst 2006). However, unlike other studies (Ims and Andreassen 2005) my analysis does not show a general securing effect of density dependent dispersal even when the model was adapted to the same experimental data. Strong synchrony can also emerge from density dependent dispersal, not only from density independent dispersal, if net emigration rates are comparable. The strength of dispersal is much more important for spatial synchrony than its dependence on density, but most important is the mechanism of density regulation (chapter 2). For the mechanisms of density regulation, my results show that peaks of spatial synchrony do not only emerge with over-compensatory but also with under-compensatory density regulation and that the relation between density regulation mechanisms and synchrony follows a bimodal rather than a unimodal relationship. However, synchrony by itself does not jeopardize metapopulation persistence but only in conjunction with high local extinction risk. Therefore, high synchrony at under-compensation has no detrimental effect, and the relation between density regulation and persistence is unimodal (chapter 1). My work on the role of density regulation in spatial single-species systems implies that high connectivity between habitat patches is beneficial for under-compensators but may be detrimental for over-compensators. It emphasizes the importance of competitive interactions and landscape connectivity for conservation planning: While dispersal corridors are essential for species with under-compensatory density regulation, they may have detrimental effects for endangered species with over-compensation (chapter 1).

Turning from the role of density regulation in single species systems to its role in two-species communities reveals a new mechanism of coexistence. Differences in the mechanisms of density regulation enable two otherwise identical species that exert equal intra- and interspecific competition strength to coexist on a common abiotic resource if at least one species exhibits over-compensation. Coexistence through over-compensation is possible because the over-compensator tends to generate fluctuations from which it suffers, whereas the competing species tends to dampen these fluctuations from which it benefits. In my theoretical investigations this new mechanism of coexistence occurs over a wide parameter range and operates especially well under light disturbance and fragmentation regimes. In the real world it is potentially relevant for communities with high species diversity but apparent limited resources, such as the small mammal and insect communities in some parts of the tropical rainforest or marine plankton communities (chapter 3).

The detection of coexistence through over-compensation as a stabilizing mechanism of coexistence is especially valuable as it allows a direct comparison with the equalizing

mechanism of neutral coexistence in the framework of density regulation. Thus, my work contributes to the recent debate on the relative roles of stabilizing and equalizing mechanisms in structuring communities. My results indicate that communities relying on coexistence through over-compensation are more likely to be found in well-connected landscapes with high habitat availability, while communities relying on neutral coexistence are more likely to be found in fragmented and isolated landscapes. Thus, community response to climatic range-shifting or landscape fragmentation sensitively depends on the underlying coexistence mechanisms. To conclude, a deeper understanding of the processes structuring communities is required to further our understanding of the potentially synergistic threats of different types of environmental change (chapter 4).

Broadening the focus to a higher number of species and applying the mechanistic model to field data, I evaluated the spatio-temporal abundance patterns of the highly diverse small mammal community of the fragmented Atlantic Forest in Brazil. I aimed at a better understanding of (1) the processes that structure this community and determine the resulting diversity, and (2) the long-term effects of forest fragmentation on local and regional species diversity. Building upon recent advances in Bayesian statistics, results demonstrate the importance of species matrix intolerance and species competitive interactions for the observed community structure and biodiversity pattern: Diversity within patches decreases with decreasing size and connectivity of forest patches, but diversity between patches increases and regional diversity remains constant. However, for the future the model predicts an increase in spatial heterogeneity for the community structure (chapter 5).

## Practical significance of the thesis

Field ecologists frequently confront me and my generic models with the questions 'what are these models good for?' and 'how are they supposed to help understanding the complex nature outside?' These questions point to a 'credibility gap' (Benton et al. 2007), i.e. to the fact that insights from model systems are often viewed as being irrelevant for understanding processes in the real world.

My first answer would be that the human mind is unable to think in other ways than in models (Wissel 1989). We need to reduce the available amount of information to what is necessary, and abstract from reality to models in order to handle the complex information we experience from the world around us. Simulation models work in a comparable way and on

the one hand enable testing hypothesis on the functioning of systems in a simplified environment and on the other hand allow analysing species systems over temporal and spatial scales that are not amenable to traditional experimental research methods. In using a simulation model, we can structure and link available knowledge and evaluate what results from the modeled entities and the rules for their changes. However, the question remains what the necessary amount of information is. Its answer depends on our research question. Studies that aim at a level of generalization that is not directly applicable to a specific system often require a relatively low level of complexity to ensure full understanding of processes and interactions. It is more or less pointless to debate on the sense of models in general. Rather, we should discuss the reasonableness of the underlying assumptions and rules and how and whether the implications of the models can be tested and generalized.

Second, the models presented in this thesis have a relatively low level of complexity and the insights from them are aimed to be applicable in a wide range of systems and communities. They belong to the class of 'minimal models for a system' (Roughgarden et al. 1996) that are 'intended to explain phenomena of certain classes of systems or species, while ignoring many characteristics of the real system in the hope they are not essential. These models are also not designed for specific, detailed predictions.' (Grimm et al. 2005, p. 367). While they ignore a number of sub-processes and structures of real-world communities, they are nevertheless able to capture some of the main landscape dynamics (habitat loss, patch connectivity, climatic range shifting) and the main population processes (density dependent growth, dispersal and density independent death due to disturbances). Their generalizability and their potential for understanding mechanisms is one of their greatest strengths, but at the expense of losing specific details and quantitative applicability. Critique in highly aggregated models of hypothetical populations and communities is as old as this type of models has been used in ecology (Simberloff 1981; Pielou 1981; Hall 1988) and many insightful replies to this critique exist (Levins 1969; Levin 1981; May 1981; Wissel 1989).

Third, the results of this thesis contribute to scientific knowledge by pointing out new cause-effect relationships within community dynamics (e.g., a new coexistence mechanism, chapter 3), by identifying the dependency of earlier results on specific assumptions (e.g., unimodal vs. bimodal relationship between synchrony and density regulation, chapter 1) and by considering and analysing the effects of new external threats (climate change, chapter 4), tying in with a sequence of earlier collaborative studies (Travis 2003; Best et al. 2007). However, new field observations and experiments are required to evaluate the generality of the findings (Benton et al. 2007). I have taken some initial steps towards this evaluation by

applying the model developed in this thesis to experimental and observational data. Using growth rates and carrying capacities derived from an experiment with Tundra voles showed that spatial synchrony emerges not only under density independent but also under density dependent dispersal (chapter 2). Processing spatio-temporal patterns of small mammal abundances in the fragmented Atlantic Forest exemplarily demonstrated how mechanistic multi-species models can be used for better understanding community dynamics (chapter 5).

For conservation policies, the value of the generic simulation models presented here lies in their potential to highlight the importance of certain processes, to make hidden assumptions underlying some general management guidelines apparent and to reveal negative side-effects of conservation actions. The results from this thesis point out that the common management strategy of establishing corridors between isolated habitat patches increases species extinction risk if density regulation is over-compensatory (chapter 1). This effect has been observed in communities of the flightless weevil, *Hadramphus spinipennis* (Schöps 2002; Johst and Schöps 2003). Furthermore, results show that fragmentation and climate change severely impact species survival, which is in strong concordance with empirical findings (e.g. Walther et al. 2002). In particular, this thesis approaches the issues of landscape fragmentation and climate change from both single species and community points of view. It demonstrates differential responses of assemblages persisting through alternative coexistence mechanisms (chapter 3) and reveals that a small-mammal community with currently stable diversity patterns may nevertheless be under the threat of increased spatial heterogeneity of its community structure in the future (chapter 5). The focus on community structure is novel.

In sum, generic simulation models are powerful tools for increasing our understanding of ecological processes, for gaining scientific knowledge and for assessing and supporting conservation policies.


## Where to go from here?


Here, I sketch some directions for further research that go beyond the research perspectives proposed in the previous chapters. I suggest a theoretical study, a microcosm experiment and an analysis of observations.

*A theoretical study*

There is an increasing recognition that successful geographic range shifts due to climate change do not only depend on dispersal abilities, population dynamics and community functioning (as explored in this thesis) but also on evolutionary processes. Recently, simulation studies on invasion biology (Edmonds et al. 2004; Klopfstein et al. 2006) showed that neutral mutations arising on the edge of a range expansion could occasionally 'surf' on the wave of advance and can thus reach high frequencies and large spatial distributions. Travis et al. (2007) complemented these findings by demonstrating similar behaviour for deleterious mutations, even when they have substantial negative effects on fitness. The authors concluded that these surfing dynamics are likely to have important consequences for the rates of spread of mutations and evolution in spatially expanding populations.

So far, analyses have been based on coupled-map lattice models that consider neither local population dynamics nor distance-dependent or conditional dispersal dynamics. However, these dynamics along with characteristics of landscape connectivity could strongly influence the speed and formation of the spreading wave and thereby modify the mutant's ability to surf. For instance, over-compensatory density regulation with its relatively high effective growth rate at low densities may promote satellite populations at the wave front.

The framework of models presented in this thesis provides a convenient method for testing these hypotheses. Neutral, deleterious and beneficial mutations can be represented by the extended Maynard Smith – Slatkin equation (1973; see also Hassell and Comins 1976) with the competition part of that equation replacing the Wallenius' noncentral hypergeometric distribution (Wallenius 1963) used in Travis et al. (2007).

*A microcosm experiment*

Small-scale experiments using 'model organisms' in microcosms can be a useful approach for analysing processes that occur on large temporal and spatial scales (Benton et al. 2007). The interplay between random genetic drift and natural selection during invasion processes as well as the coexistence dynamics of species tracking climatic range shifts are typical examples for questions where microcosm experiments are valuable. Using a microcosm experiment, Hallatschek et al. (2007) already confirmed the theoretical findings that neutral mutations at expanding frontiers can reach high frequencies and large spatial distributions without having any selective advantage and that common alleles in a population might not necessarily reflect positive selection but, instead, recent range expansions (Edmonds et al. 2004; Klopfstein et al. 2006). It would thus be possible to test whether theoretical predictions

on deleterious and beneficial mutations (Travis et al. 2007) can be supported by microcosm experiments. The experiments could further focus on the effects of different dispersal abilities, the impact of barriers in the landscape and on community dynamics emerging when more species are included in the system. They would thus allow for testing the significance of some of the theoretical findings presented in this thesis.

*An observational study*

In this thesis, I presented a Bayesian calibration of a mechanistic simulation model to analyse the importance of population growth, disturbances, species intolerance to the matrix and interactions within and among species for community structure (chapter 5). Further work should include experimental variations in landscape characteristics. In particular, the interplay between the quantity and spatial configuration of forest cover with respect to diversity should be studied: Does the relative degree of patch isolation and patch size still play a key role in persistence if overall forest cover is very low or very high?

Data for answering this question exist for the São Paulo Atlantic Plateau. Using the mechanistic model calibrated with data from Caucaia (chapter 5), parameter estimates can be updated with data from new study regions, Ribeirão Grande and Tapiraí, to reduce uncertainty in the parameter estimates and enhance the generality of the model. Moreover, virtual landscapes could be created and analyzed to examine the impacts of gradual changes in forest cover and landscape configuration.

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# Acknowledgements

What a great moment to finally write this part of my thesis! First, it means that a long desired aim is finally very close; second, it gives me the opportunity to thank all those people who supported me in many different ways and made this thesis a success. THANK YOU!

First and foremost, I want to thank Karin Johst – she initialized my Ph.D project, provided me with the freedom to develop it and with the knowledgeable guidance that was necessary to keep me on the way. She gave me continuous support in all respects and is simply the greatest supervisor I can imagine.

I am also grateful to Harald Bugmann for supervising this work and for giving critical and insightful feedback to our manuscripts. I owe thanks to Sebastian Bonhoeffer and Christian Wissel for accepting to examine this thesis.

I greatly appreciate the collaboration with Justin Travis who is greatly inspiring and teaches me the miracle of writing clear and lively texts. Renata Pardini introduced me to the world of neotropical small mammals.

I particularly owe thanks to the Oesa, my working group at the UFZ, which was part of my life for the past years. I learned a lot from the Oesians in numerous seminars, lectures and talks. However, most valuable was the great working atmosphere that gave an additional reason to go to work each morning and also connected work with a number of enjoyable side activities. This inspiring work environment would not have been possible without the influence of Christian Wissel, our former group leader. Numerous of the Oesians have contributed to this thesis with fruitful critiques and great emotional support and I especially like to thank Jula, Frank, Claudia, Michael, Ute, Oliver, Florian, Birgit, Steph, and Sandro. Andreas, Volker, and Karin I would like to thank for the many helpful discussions on 'how to survive as a scientist'.

Particular thanks go to my former office mate Jürgen, who is a great workmate and friend and with whom it was an immense pleasure to share our little spot in the Oesa. He helped me to overcome a number of obstacles on my way and taught me that an 'o.k.' talk is not a good talk.

Thomas I want to thank for many inspiring discussions and for being there. I learned a lot from you and I am – finally – very grateful for all the deleted paragraphs and all the 'no, you can't write it like this'.

I thank Björn for his patient companionship and support during my phases of great enthusiasm and desperation and for his occasional impatience when it was necessary. It is very encouraging and a lot of fun to work together with you and I am looking forward to more!

Finally, I thank the persons who have supported me longest – my family.

# Curriculum vitae

## EDUCATION

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|---|---:|
| **PhD student** | *2008* |

*University:* Forest Ecology, Department of Environmental Sciences, ETH Zurich, Switzerland

*Main working place:* Department of Ecological Modelling, Helmholtz Centre for Environmental Research - UFZ, Leipzig, Germany

*Start:* November 2004

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|---|---:|
| **Postgraduate Diploma, Applied Statistics, ETH Zurich, Switzerland** | *2007* |

*Thesis:* Habitat loss and dynamic habitat patches in fragmented landscapes: How sensitive is species coexistence?

*Supervision:* Dr. H.R. Roth, Department of Mathematics, ETH Zurich

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|---|---:|
| **Diploma, Biology, Philipps-University Marburg, Germany** | *2004* |

*Thesis:* Metapopulation survival in dynamic landscapes: Interaction of local dynamics and dispersal

*Supervision:* Dr. K. Johst and Prof. Dr. C. Wissel, Department of Ecological Modelling, UFZ Leipzig

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| **Diploma, Psychology, Philipps-University Marburg, Germany** | *2003* |

*Thesis:* Quality of life and environmental perception as functions of natural values

*Supervision:* Dr. A. Homburg, Department of Social Psychology, Philipps-University Marburg

## SCIENTIFIC ACTIVITIES & TEACHING EXPERIENCE

| | |
|---|---:|
| **YoMo activities** | *2005 - present* |

Co-founded a network for Young Modellers in Ecology (YoMos)
Developed parts of the YoMo internet presence
Co-organised the yearly YoMo Workshop in 2006, 2007 and 2008

| | |
|---|---:|
| **Advanced methods of data exploration** | *2008* |

Co-organized and taught in a ten-day course on ecological experiments, statistics and mechanistic modelling in Białowieża, Poland

| | |
|---|---:|
| **Applied statistics in Ecology** | *2007* |

Assisted and supervised an obligatory two-week module of the M.Sc. Biodiversity Management & Research at the University of Namibia

| | |
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| **Courses on applied statistics** | *2005 - present* |

Taught regular lectures at the UFZ
Taught a two-day course at the University of Marburg

| | |
|---|---:|
| **Teaching assistant for courses on applied statistics and experimental design** | *2005* |

Assisted and supervised two one-week courses at the University of Potsdam

| | |
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| **Teaching assistant for courses on ecological modelling (in C++)** | *2005, 2006* |

Assisted and supervised two one-week courses at the UFZ

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| **Teaching assistant, Philipps-University Marburg** | *2002* |

Assisted and supervised a graduate level plant-ecology course

## RESEARCH EXPERIENCE

| | |
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| Research Assistant, UFZ, Germany | *2002, 2004* |
| Field Assistant in Myanmar, Smithsonian Institution, USA | *2004* |
| Research Assistant, Philipps-University of Marburg, Germany | *2002* |
| Field Assistant, Everglades National Park, USA | *1999* |
| Research Assistant, Polish Academy of Science, Mammal Research Institute, Poland | *1998, 2000* |

## PEER REVIEWED PUBLICATIONS

Münkemüller, T., Reineking, B., Travis, J., Bugmann H. and Johst, K. (submitted): Disappearing refuges in time and space: How climate change and habitat isolation threaten species coexistence.

Münkemüller, T., Bugmann H. and Johst, K. (submitted): Hutchinson revisited: Over-compensatory density regulation promotes species coexistence on a single resource.

Zimmermann, J., Higgins, S.I., Grimm, V., Hoffmann, J., Münkemüller, T. & Linstädter, A. (in press, J. Ecol.): Recruitment filters in a perennial grassland: the interactive roles of fire, competitors, moisture and seed availability.

Münkemüller, T. and Johst, K. (2008): Spatial synchrony through density independent versus density dependent dispersal. Journal of Biological Dynamics, 2 (1): 31-39.

Travis, M.J., Münkemüller, T., Burton, O.J., Best, A., Dytham, C. and Johst, K. (2007): Deleterious mutations can surf to high densities on the wave front of an expanding population. Mol. Biol. Evol., 24 (10): 2334–2343.

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Münkemüller, T. and Johst, K. (2006): Compensatory versus over-compensatory density regulation: Implications for metapopulation persistence in dynamic landscapes. Ecol. Model., 197 (1-2): 171-178.

Münkemüller, T. and Homburg, A. (2005): Naturerfahrungen: Dimensionen und Beeinflussung durch naturschutzfachliche Wertigkeit. Umweltpsychologie, 9: 50-67.

## SELECTED ORAL & POSTER PRESENTATIONS

Münkemüller, T. & Johst, K. (2007): Density regulation and its effects on species persistence, coexistence and diversity. Talk in the working group of William Fagan, Department of Biology, University of Maryland, USA.

Münkemüller, T., Bugmann, H. & Johst, K. (2007): Hutchinson revisited: Over-compensation promotes species coexistence. Talk at the 6th European Conference on Ecological Modelling, ECEM, in Trieste, Italy.

Münkemüller, T., Fontalvo-Herazo, M.L., Meyer, K., Mosner, E., Piou, C., Schiffers, K. & Tietjen, B. (2007): Young Modellers in Ecology. Poster at the ALTER-Net All Parties' Conference in Palma de Mallorca, Spain.

Münkemüller, T., Bugmann, H. & Johst, K. (2006): Chaos schafft Artenvielfalt. Talk at the UFZ PhD Conference in Leipzig, Germany. Winner of the Award for the best talk.

Münkemüller, T., Bugmann, H. & Johst, K. (2005): Over-compensation maintains species diversity. Poster at the DIVERSITAS Conference in Oaxaca, Mexico. Winner of the 'Young Scientist Award for the best poster'

Münkemüller, T. & Johst, K. (2005): How does intraspecific competition influence metapopulation synchrony and persistence? Talk at the 35th Annual Conference of the Ecological Society of Germany, Switzerland and Austria, GfÖ, in Regensburg, Germany