Modelling the structuring of animal communities in heterogeneous landscapes – the role of individual home range formation, foraging movement, competition and habitat configuration

Carsten M. Buchmann

Plant Ecology & Nature Conservation
University of Potsdam
January 2012

Institut für Biochemie und Biologie
Arbeitsgruppe Vegetationsökologie und Naturschutz

Modelling the structuring of animal communities in heterogeneous landscapes – the role of individual home range formation, foraging movement, competition and habitat configuration

Dissertation
zur Erlangung des akademischen Grades
"doctor rerum naturalium"
(Dr. rer. nat.)
in der Wissenschaftsdisziplin "Ökologie und Naturschutz"

als kummulative Dissertation eingereicht an der
Mathematisch-Naturwissenschaftlichen Fakultät
der Universität Potsdam

von
Carsten Michael Buchmann

Potsdam, den 19. Januar 2012

Table of contents

Summary

Understanding and predicting the composition and spatial structure of communities is a central challenge in ecology. Mechanistic understanding of community structure is essential if we aim at predicting how animal communities will respond to environmental change, like for example habitat loss and fragmentation, both considered among the greatest contributors to past and future extinctions. The majority of empirical and theoretical studies, however, still focus on single species. The few modelling studies at the community scale are either not spatially explicit, and therefore not suitable to consider complex spatial landscape effects, or focus on spatial processes at large scales, like dispersal or isolation effects. However, small scale processes, like the formation of individual home ranges, which integrates physiology and behaviour (like foraging strategy) but also intra- and interspecific competition, may not be ignored because they determine how individuals perform in heterogeneous landscapes and therefore control how they will cope with changing resource distributions.

In this thesis I introduce a novel individual-based modelling approach that for the first time simulates an entire animal community on the basis of individual home range establishment in a spatially explicit way. The use of allometric relationships for individual resource needs and locomotion costs allows for modelling home range establishment, not only of a single species, but of individuals of a wide range of body masses, that coexist and compete for resources in a landscape.

In Chapter1, the model is introduced – parameterized for mammals that consume the primary production provided by a fractal grid-based landscape. Model behaviour is elucidated in dependence of major model parameters, robustness of model predictions in dependence of resource productivity is tested and the applicability of the model for the simulation of specific communities (empirical data on species body masses) is demonstrated. Besides predictions of the spatial distribution of all individual home ranges, the model produces the allometric relationship between body mass and home range size as well as the body mass distribution (specifically the individual size distribution ISD) of the community that both agree well with independent data. Results demonstrate the importance of spatial resource use and individual home ranges for the structuring of animal communities.

In Chapter 2 three fundamentally different foraging movement strategies (central place forager, patrolling forager and body mass dependent nomadic forager) are incorporated into the allometric model of home range formation, and are compared with respect to their efficiency for mammals of different body size and to the subsequent effect they have on community response to habitat loss. While central place foraging is only efficient for small animals, particularly nomadic foraging is advantageous for larger animals. This is also reflected in a delayed non-linear response of the ISD to habitat loss.

Such complex model behaviour is in detail explained in Chapter 3 where small mass windows within the size spectrum (interpreted as populations of single species) of mammal and bird communities and the effect of competition are analysed. For mammal and bird communities body mass dependent competitive release effects can explain the response of the ISD with increasing habitat loss. In contrast, habitat fragmentation shows a different effect on mammals and birds. While generally having a strong negative effect on mammal abundance, the release from heavier competitors can even lead to a positive effect of habitat fragmentation on small mammals. In contrast, bird abundance is hardly affected because they can buffer fragmentation effects by adapting the size of their home ranges.

Taken together, these results display that it is possible to scale from individual physiology and behaviour to the structure of animal communities. Doing so, the model represents a new way to mechanistically explain community structure, generates hypotheses about spatial community structure and landscape effects on communities, and gives guidance to future empirical and theoretical research. Results, moreover, demonstrate potentially strong effects that foraging strategy and space use as well as competition have on community response to landscape changes and therefore emphasize the importance to consider these processes for effective conservation management of animal communities.

General introduction

0.1 Motivation – understanding community structure

The question which mechanisms are the relevant ones structuring ecological communities has a long history in community ecology (e.g. Motomura 1932, MacArthur 1960, May 1975, Holling 1992, Hubbell 2001). Gaining such a mechanistic understanding is essential particularly if scientists and conservation managers are interested in how communities will respond to environmental changes. Many studies have yielded valuable information and increased our knowledge on relevant processes; however, most research is still limited single species. In this thesis I will introduce a new mechanistic modelling approach in order to increase our understanding of communities of interacting species and how they are affected by landscape changes.

0.1.1 On the composition of terrestrial animal communities

Simple community patterns that have received much attention are the diversity of communities (how many species are present) or the abundance distribution of species that are present in a community. In order to describe these basic patterns simplistic theories and models were applied, ranging from purely statistical ones, such as the lognormal distribution (Preston 1948), over niche partitioning theories like the geometric series (Motomura 1932) or the famous broken stick model by MacArthur (1957), to the unified neutral theory of biodiversity and biogeography (Hubbell 2001, 2006; see McGill et al. 2007 for an extensive review and categorization of different generations of theories and models). The phenomenological models, but also the broken stick model and the geometric series, were used to describe rank-abundance patterns in communities, however, without supplying any specific and solid mechanistic basis (Loehle 2006). The other prominent but simplistic concept to explain species diversity and relative abundance distributions in communities, the unified neutral theory of biodiversity (Hubbell 2001), considers all species to be equal. Here, dynamics in species distribution and abundance are controlled by random migration (dispersal), speciation and extinction, and species-specific properties or traits are assumed to not be relevant.

More structural and functional information about communities is contained in community measures that also consider species traits. A key functional trait, and probably the most ecologically integrative attribute of animals is their body size, since almost all physiological and many ecological properties are clearly correlated with it (Allen et al. 2006). Such correlations are well described by allometric relationships, which are power functions of the form

$$Y = Y_0 \times M^b , \qquad (0.1)$$

where Y is some dependent variable (like for example metabolic rate, bite size or home range size), b is the allometric exponent and Y_0 is a normalization constant (e.g. West et al. 2002, Brown et al. 2004). Because body mass is so influential for individuals the distribution of body mass in natural systems has been studied intensively. Much work has been done on the number of species within a certain body size class, either at global or continental scales or coexisting in local assemblages (e.g. Lawton 1990, Brown and Nicoletto 1991, Blackburn and Gaston 1994, Brown 1995, Allen et al. 2006). Different arguments have been applied to explain and understand observed patterns, ranging from evolutionary and physiological reasons to competition and dispersal (reviewed in Allen et al. 2006).

Another abundance - body size pattern that received much attention is the abundance of species of certain body size (often called the ‘population density plot’ by Damuth 1981a, 1987). A prominent explanation for the slope of this relationship of around -0.75 in a double logarithmic plot, which is equal to the allometric exponent (see Eq. 0.1) is the so-called ‘energy equivalence rule’ by Damuth (1981a, 1987, White et al. 2007). The basis of this rule is the fact that metabolic needs of individuals scale with 0.75, i.e. reciprocal to population density. The rule therefore states that each population in a communtiy can access and subsequently consumes approximately the same amount of resources.

Because in natural communities individuals are the entities that act and interact (and not species), a combination of the two measures, species number and population density of these species over body mass, which hence integrates mechanisms taking place at the individual level, therefore seems to be a more appropriate measure characterizing communities (see also Ernest 2005). Such a combination would be the individual size distribution (ISD) of a community, which, in contrast to aquatic systems, is still rarely studied in terrestrial communities (White et al. 2007, but see Reuman et al. 2008).

0.1.2 Communities in space – in face of landscape modifications like habitat loss and fragmentation

In addition to this compositional structure, terrestrial animal communities are strongly structured in space. Spatial processes, such as dispersal, space use and movement, resource use and species interactions in space or territoriality play a major role in structuring terrestrial communites (e.g. Wiegand et al. 2000, Yaacobi et al. 2007, Jeltsch et al. 2008, Hibert et al. 2010). Understanding these processes and their interplay, and how they control community structure, becomes increasingly important if we want to investigate the impact of (mostly man-made) landscape modifications on animal communities. The loss and fragmentation of suitable habitat are considered among the largest threats to natural communities and the greatest contributors to the ongoing loss of biodiversity on earth (Andren 1994, Henle et al. 2004). While effects of reduced habitat area (habitat loss) on populations are quite consistent and are rather well understood, the effects of fragmentation are mostly weaker and often contradictory (for clarification: the term ‘fragmentation’ is here used to describe the spatial configuration of habitat only, while total habitat area remains constant; Andren 1994, Fahrig 2003). Habitat loss is considered to generally affect populations negatively. Various theoretical studies have proposed different mechanistic explanations (from percolation theory to Allee effects) for frequently observed threshold behaviour of population size with habitat loss (for reviews see Harrison and Bruna 1999, Fahrig 2002, Swift and Hannon 2010). Reported effects of fragmentation, however, encompass positive and negative effects, as well as no effect, on populations (Fahrig 2003, Smith et al. 2011). Particularly the interaction of the effects of the two spatial factors causes extra complexity and therefore represents a difficult challenge for scientists and conservation managers.

Because empirical investigation of entire communities is costly and hardly manageable, most studies only consider impacts of landscape modifications on certain species, including effects on species abundance and distribution but also considering behaviour and sociality (e.g. Bowers et al. 1996a, Said and Servanty 2005, Norris et al. 2010). Even if other authors make use of the various findings to draw more general conclusions about the effects of landscape changes on communities (Fahrig 2003, Henle et al. 2004, Banks et al. 2007), the mechanistic understanding of how interacting communities respond to habitat loss, to fragmentation and the combination of the two, is still rather poor.

In recent years various modelling approaches have been developed in order to investigate how populations in communities and also entire communities of interacting species respond to environmental changes (e.g. Vucetich et al. 1997, Domis et al. 2007, Wilmers et al. 2007). The majority of models that address the effects of spatial factors (like habitat loss and fragmentation) on communities belong to the group of metacommunity models (spatially implicit: e.g. Kadmon and Allouche 2007, Economo and Keitt 2008, and spatially explicit: e.g. Büchi et al. 2009, Filotas et al. 2010; see Flather and Bevers 2002, Leibold et al. 2004, Hawkes 2009 for more detailed description and categorization of such models). Generally all these models are designed to focus on processes at larger temporal and spatial scales, so that single localities, often also called patches, can hold entire local communities which are connected via dispersal of the different species. Hence, dispersal (specifically for animals: emigration and immigration) is the only crucial spatial processes that is explicitly considered in these models and which is influenced by spatial habitat configuration.

However, processes at a smaller scale, like foraging movement and behaviour or local resource use and competition in communities strongly control how individuals manage to cope with changing landscape characteristics (e.g. Nee and May 1992, Ritchie 1998, Ritchie and Olff 1999, Banks et al.2007, Bassett and Angelis 2007, Hawkes 2009, Pita et al. 2010). These spatial processes, therefore play a major role for the performance of individuals, populations and communities, and must not be ignored when we are aiming at a better understanding of community response to habitat loss and fragmentation.

0.1.3 The importance of home range for understanding terrestrial communities

Terrestrial animals, like mammals or birds generally occupy specific areas, their home ranges (Burt 1943), which are relatively stable during certain life phases. The establishment and subsequently the size and location of a home range is on the one hand determined by landscape properties, particularly the distribution and availability of resources. On the other hand animal physiology and behaviour, specifically movement, as well as inter- and intraspecific interactions are crucial determinants of this highly integrative ecological variable (e.g. Damuth 1981b, Holling 1992, Börger et al. 2008). The distribution of individual home ranges in a community can therefore be interpreted as a spatially explicit fingerprint of these (small scale) mechanisms that are of great relevance for the structuring of animal communities.

Given these arguments, it seems more than obvious that gaining a mechanistic understanding of home range formation in communities is on the one hand a difficult challenge, but on the other hand a key requirement for a thorough elaboration of terrestrial communities. Considering the serious threats to communities and ecosystems by actual landscape modifications (i.e. spatial effects), the role of home ranges needs even more emphasis. Individual-based models have proven to be suitable to simulate home ranges as the consequence of explicit movements of individuals in space in response to other individuals and the environment (e.g. Wiegand et al. 2004, Moorcroft et al. 2006, Wang and Grimm 2007). Individual-based models are in general suitable for investigating multi-species systems (Basset and Angelis 2007). However, like empirical investigation of home ranges (Bowers et al. 1996a, Said and Servanty 2005, Carfagno and Weatherhead 2008), most mechanistic individual-based home range models are still dealing with only one target species and are therefore case studies (e.g. Bowers et al. 1996b, Wiegand et al. 2004, Moorcroft et al. 2006, Wang and Grimm 2007). Two exceptions are more general approaches, one based on movement and memory of individuals, recently presented by Van Moorter et al. (2009) and a second much simpler approach of Mitchell and Powell (2004) which relates patch selection of individuals in an optimal foraging framework to home range formation. However, even if not designed for a specific species both approaches still focus on intraspecific interactions and disregard the diversity of species in communities.

The only community pattern of individual space use that has attracted much attention of ecologists during the last decades is the allometry of home range size (compare Eq. 0.1). There is general agreement on that the exponent of this relationship is approximately 1 while the coefficient varies between taxa and trophic levels (e.g. Kelt and Van Vuren 2001, Jetz et al. 2004, Hendriks et al. 2009). In face of the prevalent assumption that home ranges are primarily resource controlled and resource requirements of animals scale with $M^{0.75}$ (Nagy 2001), this had lead to a lively debate about the reasons for the observed scaling of home range size over years. The question discussed is: what are the reasons that heavier animals have larger home ranges, compared to smaller animals, than one could expect from their higher metabolic requirements alone? Proposed explanations range from stronger home range overlap of larger animals (Damuth 1981b), lower resource availability of larger animals (Harestad and Bunnell 1979) explained by fractal characteristics of resource distributions (Holling 1992, Haskell et al. 2002) and higher dietary specialization of small animals (Brown and Maurer 1989) to effects of biological times in relation to spatial requirements of animals (Lindstedt et al. 1986) and stronger spatial constraints on home range defence of larger animals (Jetz et al. 2004). This discussion about the discrepancy in scaling exponents of 0.25 is still not solved (particularly consider the criticism of Makarieva et al. 2005 on the reasoning of Jetz et al. 2004). This demonstrates the complexity of individual resource use in space in consideration of intra and interspecific interactions and reveals the lack of knowledge we still have and the urgent need to develop mechanistic home range models for animal communities.

Because all those (body mass dependent) processes controlling animal home range also affect abundance the two variables are obviously clearly linked. However, the relationship between the allometric scaling of home range size and the scaling of individual abundance (ISD, see above) has still not been paid much attention to. Stability, particularly the presence and the frequency of disturbances, of the ecosystem is discussed by Makarieva et al. (2005) in the context of metabolic requirements and resource use of species and the two community patterns, the allometries of home range and population density (abundance of species present per area). The authors consider the body mass scaling of abundance to be more strongly affected by disturbance than home ranges, because the latter are interpreted to integrate animal genetics, morphology and behavioural aspects which are not directly affected by disturbance.

0.1.4 Small scale processes – their role for home range and community structure

As already mentioned above, mechanistic home range models are particularly well suited to investigate questions of spatial factors (for example habitat configuration) on populations or communities, because home ranges, including the search and establishment of home ranges, integrate important spatial processes. In particular individual movement is a central process since it determines to what subset of environmental heterogeneity individuals are exposed, and subsequently controls local resource use and competition between individuals in space. As resource use is strongly linked to individual fitness, Morales et al. (2010) described movement as a bridge between behaviour, landscape ecology and population dynamics. In recent years more and more studies address different aspects of animal movement. The need for a deep examination of the manifold topic paved the road for 'movement ecology' as a new discipline in Ecology (e.g. Holden 2006, Nathan et al. 2008). Different studies focus on movement decisions, step lengths, turning angles or different movement modes and relate movement to population performance considering the spatial landscape context (Aars et al. 1999, Russel et al. 2003, Fryxell et al. 2008, Romero et al. 2009, Leblond et al. 2010). Various models were developed to explain individual movement paths and to raise the understanding of individual foraging strategies and space use patterns (e.g. Morales et al. 2004, Scharf et al.2006, Nonaka and Holme 2007, Skorka et al. 2009; for reviews see for example Börger et al. 2008, Patterson et al.2008, Owen-Smith et al. 2010). However, similarly to empirical and theoretical studies on individual home range movement ecology is to date still limited to individuals or populations of single species. A major reason for this is that most approaches are rather complex and therefore hardly simultaneously applicable to individuals of different interacting species.

As the role of individual movement is so prominent, it is, however, obviously required to also incorporate aspects of individual movement into the investigation of communities (Ernest et al. 2008). There is particular need to do so for small scale, within home range, movements associated with foraging behaviour (see above). Such space use behaviour, which can also differ in dependence of the taxon considered, for example higher mobility and larger home ranges in birds than in mammals (Ottaviani et al. 2006), can be expected to strongly affect not only single populations but also communities, and to mediate the effect of landscape changes on these communities. Space use characteristics of species vary, also in dependence of species body size, for example foraging modes or the size and traversing frequencies of home ranges (Swihart et al. 1988, Benhamou 1996, Jetz et al. 2004). One can therefore expect that different species (with different body masses) show a different response to changing resource landscapes. This, in turn, would affect the characteristics and strengths of interspecific interactions within the community which would itself again reveal an effect on the different species.

The complexity of these scenarios demonstrates how little we still understand of how small scale processes, like foraging strategy, including foraging movement, behaviour, local resource use and competition control community structure. Mechanistic understanding of how the interplay of such mechanisms determines the distribution and characteristics of individual home ranges in dependence of landscape properties, and subsequently community structure, is urgently needed because it would help to assess the susceptibility of communities to habitat loss and fragmentation. Summarizing the above, a mechanistic and spatially explicit modelling concept, based on the formation of individual home ranges in a community of interacting individuals (thus, incorporating all the small scale mechanisms mentioned above) appears to be the most promising instrument to address this fundamental challenge in community ecology.

0.2 Objectives of the thesis

This thesis has the objective to increase our mechanistic understanding of the processes that control the structure of terrestrial animal communities. Understanding the interplay of relevant processes is essential for effective conservation management in face of environmental change. However, previous approaches are either i) not spatially explicit and therefore not able to depict complex effects like habitat loss, fragmentation of available habitat area or a combination of the two, or are ii) only applicable for single species at a time and therefore not useful to analyse communities of interacting individuals of different species, or are iii) focussing only on large scale processes like dispersal and ignore small scale (within home range) processes like individual foraging movements and local resource competition in space.

In this thesis I will present a new modelling approach that circumvents all these three shortcomings by simulating communities on the basis of the establishment of individual home ranges in an individual-based and spatially explicit way. Because home ranges integrate animal physiology, resource use and behavioural aspects, a mechanistic model of home range formation can account for all these mechanisms and test for their role in controlling species performance in light of landscape changes. As the model aims at simulating home ranges of individuals of an entire community and not only a single species, it will be possible to explore how the interplay of these mechanisms affects spatial as well as compositional community structure. Using this new modelling approach also offers the possibility to ‘zoom into the mechanisms’, and, for example explore the competition structure within the community. Using realistic grid-based simulation landscapes that can be varied not only with respect to the amount of habitat area but also with respect to the level of fragmentation of this habitat (few large habitat vs. many small habitat patches, controlled by spatial autocorrelation) moreover allows the mechanistic investigation of communities in light of changing landscape structure.

In order to allow the parameterization not only for a single species but for an entire community a model has to be simplistic by describing interspecific variation in relevant processes in a generic rather than idiosyncratic way. While common individual-based approaches are difficult to parameterize for different species because of their complexity, trait-based approaches are advancing fast in community ecology (McGill et al. 2006). Their advantage is that they allow simplification and generalization by reducing system complexity to traits that are applicable to all species of interest. Body size is one of the most important and meaningful functional traits of animals as it determines inter- and intraspecific variation in most physiological and many ecological properties through allometric relationships. The application of well established allometric relationships in order to paramterize the new modelling framework introduced in this thesis, allows scaling from individual physiology and behaviour to an entire community of interacting animals. Moreover, the simplistic modelling concept permits the application to mammal and bird communities. Specific questions that are addressed in this thesis are:

1. Is such a generic model able to independently produce realistic relationships between body size and home range size as well as abundance, i.e. two complex community patterns, at once?
2. How robust are such predictions to varying landscape resource productivity and distribution?
3. How does foraging strategy implemented in the model affect community structure and the community response to landscape changes?
4. How do mammal and bird communities respond to habitat loss and fragmentation, alone and in combination, and what role do space use characteristics and competition play for the observed responses?

0.3 Outline of the thesis

Given the cumulative format of this thesis, the three chapters of the thesis were prepared as separate and independent articles for publication in scientific journals. They are written in first person plural because they are co-authored. For all three chapters I have implemented the model, conducted simulations and analysed the results by my own – co-authors supported me developing the modelling concept and analysis methods and commented on the three chapters which helped improving the manuscripts. Since Chapters 2 and 3 are based on a model which is introduced in Chapter 1 all three chapters contain overlapping information, particularly in the methods sections. They can therefore be read independently. In this thesis the chapters are connected with intersections.

In Chapter 1 I introduce the new allometric modelling approach to explain the structure of mammal communities, specifically the body mass scaling of abundance and home range size, on the basis of individual home range formation in heterogeneous environments. In Chapter 2 I apply and extend the allometric model to investigate the role of foraging strategy for community structure in the face of habitat loss. In Chapter 3 the modelling approach is additionally adapted to birds, which allows employing the model to explore effects of habitat loss and fragmentation on mammal and bird communities. Here, a special focus is given to individual space use and interspecific competition within the community in order to explain predicted patterns.

The thesis is completed with a brief general discussion of the major results and of the advantages and limitations of the chosen approach. In this discussion I will also give an outlook on possible directions for further research and summarize the main conclusions of the thesis.

Chapter 1

A new allometric model explains the structuring of animal communities in heterogeneous landscapes

A version of this chapter is published as: Buchmann, C. M., Schurr, F. M., Nathan, R. and Jeltsch, F. (2011) An allometric model of home range formation explains the structuring of animal communities exploiting heterogeneous resources. *Oikos*, **120**, 106-118.

1.1 Abstract

Understanding and predicting the composition and spatial structure of communities is a central challenge in ecology. An important structural property of animal communities is the distribution of individual home ranges. Home range formation is controlled by resource heterogeneity, the physiology and behaviour of individual animals, and their intra- and interspecific interactions. However, a quantitative mechanistic understanding of how home range formation influences community composition is still lacking. To explore the link between home range formation and community composition in heterogeneous landscapes we combine allometric relationships for physiological properties with an algorithm that selects optimal home ranges given locomotion costs, resource depletion and competition in a spatially explicit individual-based modelling framework. From a spatial distribution of resources and an input distribution of animal body mass, our model predicts the size and location of individual home ranges as well as the individual size distribution (ISD) in an animal community. For a broad range of body mass input distributions, including empirical body mass distributions of North American and Australian mammals, our model predictions agree with independent data on the body mass scaling of home range size and individual abundance in terrestrial mammals. Model predictions are also robust against variation in habitat productivity and landscape heterogeneity. The combination of allometric relationships for locomotion costs and resource needs with resource competition in an optimal foraging framework enables us to scale from individual properties to the structure of animal communities in heterogeneous landscapes. The proposed spatially explicit modelling concept not only allows for detailed investigation of landscape effects on animal communities, but also provides novel insights into the mechanisms by which resource competition in space shapes animal communities.

1.2 Introduction

Resource availability is a key factor controlling animal populations and communities (Richie and Olff 1999, Basset and Angelis 2007, Carbone et al. 2007, Damuth 2007). In heterogeneous landscapes, the interplay of resource distribution, animal physiology, behavior, intra- and interspecific interactions structures animal populations and communities by shaping the distribution of individual home ranges (Damuth 1981b, Börger et al. 2008). For any given landscape the distribution of individual home ranges can thus be regarded as a spatially explicit ‘fingerprint’ of the mechanisms that structure animal communities. So far, most models of animal communities are non-spatial or spatially implicit and neglect requirements for establishment of individuals’ home ranges (Ritchie and Olff 1999, Brown et al. 2004, Carbone et al. 2007, Damuth 2007). While these models have yielded valuable insights into mechanisms affecting single community patterns (e.g. scaling of population density), they are constrained in the ability to explore the effect of landscape heterogeneity on community structure. Mechanistic, spatially explicit models describing home range formation in animal communities are therefore needed both to understand how animal communities assemble in heterogeneous landscapes and to assess how they respond to habitat change.

In recent years, a number of mechanistic individual-based home range models have been formulated that simulate home ranges as the result of spatially explicit movements and decisions of individual animals in response to each other and their environment (Wiegand et al. 2004, Moorcroft et al. 2006). Most of these models focus on specific species and case studies (Moorcroft et al. 2006, Wang and Grimm 2007). One of the few exceptions is a recent general home range model that is based on the movement and memory of individuals (Van Moorter et al. 2009). Another generic but simpler approach relating home range establishment to the spatial distribution of limiting resources was introduced by Mitchell and Powell (2004). Assuming that resources are the main factor determining animal movement, they test how basic principles of patch selection (resource maximization vs area minimization) affect home range distribution. The approach accounts for locomotion costs and incorporates a factor for food competition in overlapping home ranges. However, this and all other previous studies focused on intraspecific competition and ignored how interspecific interactions shape home range distributions. Thus, the link from individual home range formation to community structure has not been made yet. This seems remarkable since the assumption that home ranges are mainly resource controlled implies that their formation is shaped by interspecific competition between species exploiting the same resource (Basset and Angelis 2007, Banks et al. 2007).

A model describing the composition and home range distribution of an entire animal community has to fulfil two criteria: i) it has to describe both intra- and interspecific competition for resources affecting home range selection, and ii) for the model to be parameterized for species-rich communities, it has to describe interspecific variation in relevant processes in a generic rather than idiosyncratic way. In principle, individual-based approaches are suitable for investigating multi-species communities (e.g. Basset and Angelis 2007). However, these models are typically difficult to parameterize because they describe each species through an idiosyncratic set of parameters. To circumvent this problem, a trait-based research programme has recently emerged in community ecology (McGill et al. 2006). Rather than focusing on species identity, the trait-based approach aims to understand the performance of organisms from their functional traits. A key functional trait is body size which determines both intra- and interspecific variation in individual properties through allometric relationships (West et al. 2002, Brown et al. 2004; for an exemplary application in modelling approaches see Bassett and Angelis 2007). Allometric relationships between body size and physiological measures such as metabolic rates (West et al. 2002), properties such as step length or bite size (Calder 1996, Shipley 2007), or biological times and rates (Brown et al. 2004), have been studied intensively and are well established.

In this study we present a novel spatially explicit, trait- and individual-based model that predicts the spatial structure and composition of animal communities in heterogeneous landscapes as the outcome of individual home range establishment. It combines available knowledge about the allometry of physiological processes with principles of optimal foraging and the home range concept. We parameterize the model with allometric data for terrestrial mammals and use it to simulate emerging home range distributions in fragmented landscapes. Specifically we ask: does this simple model independently produce realistic relationships between body mass and i) home range size and ii) abundance, i.e. can it explain two complex community patterns at once, iii) how robust are the predicted relationships to changes in resource availability and landscape heterogeneity, and iv) what lessons can be learned about the role of spatially explicit, interspecific resource competition in shaping animal communities.

1.3 Methods

In the following, we describe the structure of the model and its parameterization for herbivorous and omnivorous terrestrial mammals, the generation of landscapes used in simulations, and the simulation design. The model consists of three basic steps (Fig. 1.1):

1. An animal is assigned a specific body mass drawn at random from an input distribution.
2. For this animal, all suitable grid cells (i.e. cells with available resources) are tested as potential central cells of a home range. For each of these potential central cells, grid cells at increasing distances are added to the potential home range until this home range fulfils the animal’s energy requirement or until a maximum home range size (based on empirically

derived limits) is exceeded. For each added cell resource gain and locomotion costs are balanced (both scaling allometrically).

3. After all possible cells in the landscape have been tested as home range centre and if at least one suitable home range could be found, the animal is assigned the smallest of them and the resources in this home range are depleted.

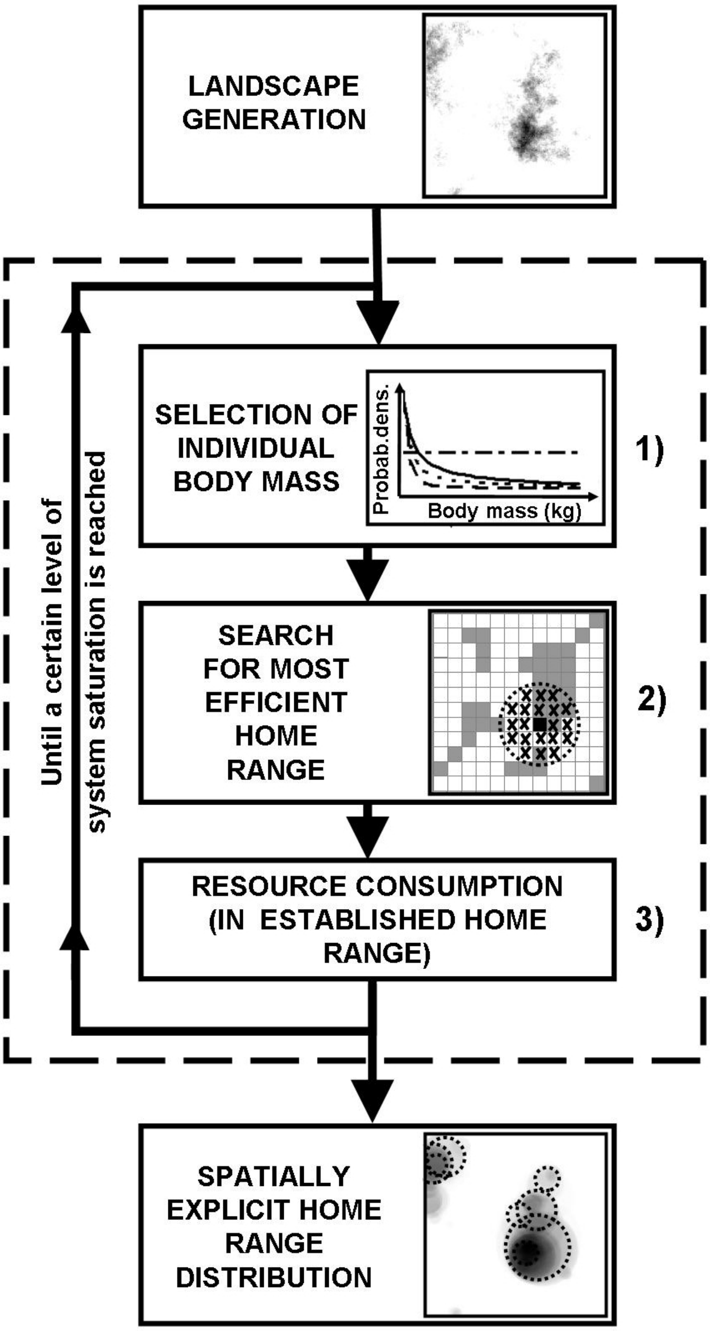

Figure 1.1. Flow chart showing the main elements of the allometric model for home range formation in animal communities.

Steps 1-3 are repeated until a certain level of system saturation (in terms of the number of animals) is reached. Technically this is implemented by terminating the simulation once a certain number of individuals failed consecutively in finding a suitable home range.

In a nutshell, our model assumes that individuals are characterized solely by their body mass, which defines energy requirements and movement costs. Moreover, we assume that all individuals use the same food resource. This means that we model a single trophic level, mammals eating plant material (i.e. herbivores and predominantly herbivorous omnivores) and ignore trophic niche differentiation. This simplification appears to be a reasonable starting point considering the principle of parsimony. Home ranges are circular and are controlled by the distribution of resources and resource competition (compare e.g. Said and Servanty 2005). We apply an area minimization principle (Mitchell and Powell 2004) corresponding to the time minimization principle in optimal foraging theory. Thus, animals 'choose' the smallest possible home range available in the entire simulation landscape. All energetic costs and benefits are balanced on a daily basis.

1.3.1 Landscape generation

Realistic fractal landscape patterns were generated using the well established midpoint displacement algorithm (Saupe 1988). This algorithm creates three-dimensional 'neutral' grid-based landscapes (With 1997) that are characterized by two parameters: the Hurst-factor H (determining spatial autocorrelation) and σ^2 (variance in displacement of points). The z-values of the landscape grid are interpreted as resource productivity.

For the simulations we tested three different levels of landscape fragmentation ranging from highly fragmented to highly clumped habitats (i.e. H = 0.1, 0.5 and 0.9, respectively, which corresponds to fractal dimensions D of 2.9, 2.5 and 2.1; σ^2 = 30 for all landscapes). For each level of fragmentation we produced five replicate landscapes of 257 × 257 grid cells. We assume that grid cells cover an area of 10 × 10 m, so that the grid has an extent of 2.57 × 2.57 km (~ 6.6 km^2). To describe landscape fragmentation we set the lowest 85% of all z-values to 0 so that 15% of the overall area remains as suitable habitat with positive resource productivity (~ 1 km^2).

The z-value of each cell i represents daily biomass production R_i, and is scaled to yield an average production across the suitable habitat of the landscape of 0.25 kg dry biomass × m^{-2} × year^{-1} (equivalent to an average of 6.85 × 10^{-2} kg dry biomass × grid cell^{-1} × day^{-1}). This reflects the productivity of typical shrublands and grasslands (Whittaker 1975). To account for competition with other taxonomic groups, and for the fact that part of the resource is not suitable for animal consumption, only a defined share (PC) of the produced biomass is available to the simulated animal community (see below for how the parameter PC is tested systematically).

1.3.2 Selection of individual body mass

Individual animals are characterized by their body mass (M), which can vary between 0.005 and 100 kg, a range covering most vertebrates. At the beginning of each iteration step an animal is assigned a body mass drawn from a continuous input distribution. We tested two different body mass input distributions for the given range of body masses,

1. a power law distribution of the form

   $$p(M) = \kappa \times M^{\eta} \qquad (1.1)$$

   with p representing the probability density of a certain body mass M. The normalization constant κ was chosen so that equation 1.1 integrates to 1; note that for a η of 0 this yields a uniform distribution;

2. empirical body mass distributions of 16 North American and Australian mammal communities, where the frequency of a species' body mass is proportional to the species' abundance.

For the range of tested values, interpretation of the theoretical distributions and references see 'Simulation design' and 'Analysis of simulation results and model validation'. Based on the individual's body mass, the model calculates the feeding rate, locomotion cost, and maximum home range size using well established allometric relationships.

1.3.3 Search for most efficient home range

For each animal, all suitable grid cells are tested for their potential to serve as the centre of a circular home range. Starting with the closest neighbouring cell and assuming periodic boundary conditions the animal gains energy in all suitable cells around the possible centre until the daily energy requirement is fulfilled. The latter is calculated as the daily field feeding rate FR which, according to Nagy (2001), scales for all mammals as

$$FR = 0.055 \times M^{0.74} \qquad \text{(kg dry biomass} \times \text{day}^{-1}\text{, M in kg).} \qquad (1.2)$$

Daily energy gain of an individual IG_i in each cell i, expressed as equivalent amount of dry biomass, is calculated as the part of the daily productivity in each grid cell which is available to the community ($R_i \times PC$) multiplied by a factor PI accounting for the part of the available resources in a cell that are exploited on daily average by the individual in case of home range establishment.

$$IG_i = R_i \times PC \times PI \qquad \text{(kg dry biomass).} \qquad (1.3)$$

This distinction between resource availability to the overall community and the fraction that can be used by individuals is necessary to test for possible allometric effects of resource availabilities and use (Damuth 1981b, Jetz et al. 2004).

Resource availability in the context of home range size (as the parameter PI) is discussed to be dependent on body mass (Harestad and Bunnell 1979). For example, large animals are believed to perceive resources at a lower resolution compared to small individuals due to fractal characteristics of resource distributions (Holling 1992, Haskell et al. 2002). This effect was used to explain observed discrepancies between the scaling of metabolic needs (exponent of 0.75) and home range size, scaling with an exponent of around 1 (Haskell et al. 2002). With regard to the model parameter PI this would mean an allometric scaling with an exponent of -0.25:

$$\mathrm{PI} = \gamma_{\mathrm{PI}} \times \frac{\mathrm{M}^{-0.25}}{0.001\mathrm{kg}^{-0.25}} \qquad \text{(M in kg)}, \qquad (1.4)$$

where the coefficient γ_{PI}, determining the general magnitude of PI, is a systematically tested model parameter. The denominator (0.001 $\mathrm{kg}^{-0.25}$) was chosen to ensure that PI varies between 0 and 1.

Other mechanisms proposed to explain the discrepancy between the scaling of metabolic needs and home range size that would lead to the same scaling of PI include the fact that larger animals face stronger spatial constraints on home range defence, effects of biological time in relation to spatial requirements of animals, social grouping, home range traversing frequencies, or food quality and specificity (summarized in Kelt and Van Vuren 2001 and Jetz et al. 2004).

The net energy gain of individuals IGN_i in each cell i is calculated as

$$\mathrm{IGN}_i = \mathrm{IG}_i - \mathrm{LC}_i \qquad \text{(kg dry biomass)}, \qquad (1.5)$$

where LC_i, are the locomotion costs of travelling to cell i expressed in equivalent amounts of dry biomass. Allometric relations for movement costs per unit distance MC are given in Calder (1996):

$$\mathrm{MC} = 10.70 \times \mathrm{M}^{0.68} \qquad (\mathrm{J} \times \mathrm{m}^{-1}, \text{ M in kg}). \qquad (1.6)$$

We convert MC into the locomotion cost LC_i of reaching grid cell i, using

$$\mathrm{LC}_i = \frac{\mathrm{d}_i \times \mathrm{MC}}{\mathrm{f}} \qquad \text{(kg dry biomass)}, \qquad (1.7)$$

where d_i is the average movement distance to cell i, assuming that each cell is visited on average once per day, and f is a conversion factor which for non-fermenting herbivores is 1.00×10^7 J × kg dry biomass intake^{-1} (Nagy 2001), neglecting possible small difference for omnivores consuming plant diet. The average distance d_i is determined as the distance between cell i and the home range centre, which is a proxy for the average distance between cell i and all cells of the home range (Mitchell and Powell 2004).

Cells are sequentially added to the potential home range until the animal is satiated ($\sum IGN \geq FR$), or until the required area exceeds a maximum home range size. This upper limit is calculated for each body mass as the maximum of

$$HR_{max-herb} = 56.23 \times M^{0.91} \quad \text{(ha, M in kg), and} \qquad (1.8)$$

$$HR_{max-omn} = 47.86 \times M^{1.18} \quad \text{(ha, M in kg),} \qquad (1.9)$$

given in Kelt and Van Vuren (2001) as the maximum of a constraint space of home range area for herbivores (Eq. 1.8) and omnivores (Eq. 1.9), both groups consuming the primary production in the model. This maximum home range limit was implemented for pragmatic reasons as it markedly reduced simulation time. Note, however, that the limit has negligible effects on model predictions: for n = 56 scenarios leading to realistic communities (compare Fig. 1.3) we conducted simulations without the limit and found that only 0-4% (median 0%) of animals established home ranges above the limit. Exclusion of these animals changed the three major output quantities by less than 2.3% (median: 0%).

If a potential home range fulfils an animal's resource requirements within the limit, the algorithm records the area and location of this potential home range. Once all suitable cells have been tested as home range centre, the animal settles in the smallest possible home range.

1.3.4 Resource consumption in established home ranges

Once an animal has established a home range, the resources in cell i of the home range are reduced by IG_i (the resources the animal uses in cell i). Subsequent animals thus encounter a landscape with partly reduced food availability. This describes competition for resources in overlapping home ranges (overlapping circular home ranges are illustrated in Fig. 1.1).

1.3.5 Assembly of home ranges in a community

Since animal communities cannot be assumed to be completely saturated (compare e.g. Starzomski et al. 2008), simulations were stopped when a defined saturation level was reached. For each combination of a specific input distribution and PI the number of animals in the simulated community shows a specific saturation response and approaches an upper limit with increasing model runtime. We used the ratio between the actual number of animals in a simulation and this upper limit as a model parameter (SATan) to describe the degree of landscape saturation or 'community packing' for each scenario. As termination criterion for simulations we used the number of consecutively failing animals (CFA) corresponding to certain saturation levels.

Saturation in terms of animal numbers (SATan) shows a strong negative correlation with the proportion of available resources that is not consumed by the community (Spearman's correlation coefficient ranges between -0.89 and -0.97 for all tested input distributions). Appendix 1.A describes in detail how the saturation approach (using SATan) is implemented.

1.3.6 Simulation design

To investigate the behaviour of the model, we conducted an extensive factorial sensitivity analysis. In this sensitivity analysis, we varied the exponent of the body mass input distribution (Eq. 1.1), testing the values -1.8, -1.6, -1.4, -1.2, -1 and 0, respectively (where an exponent of 0 yields the special case of a uniform distribution). This scope represents the range from the most basic assumption (uniform distribution, i.e. no body mass dependence of colonization potential) to distributions with exponents that can be expected in regional and local communities. We varied the percentage of biomass that is useable by individuals (by varying γ_{PI} from 4×10^{-2} to 16×10^{-2} in steps of 2×10^{-2}), and the level of saturation (SATan). For quickly saturating scenarios with power law input distribution SATan was varied between 0.99 and 0.85; for slowly saturating scenarios with uniform input distribution this range was extended down to 0.3. In further analyses, we only considered simulations that reached these saturation levels with a reasonable number of consecutively failing animals (CFA) (Appendix 1.A). Five different landscapes with the same fractal properties (H and σ^2) were used in replicate simulations for each parameter combination.

For the scenarios mentioned above the percentage of landscape resources available to the community (PC) was set to 0.2. We also systematically examined the influence of community accessible resources for a set of 10 scenarios, randomly chosen from those that yielded results in line with empirical findings. PC was varied from 0.1 to 0.4, resulting in an average level of community resources across productive area of the landscape between 0.025 and 0.1 kg dry biomass $\times$ m^{-2} $\times$ year^{-1}. Thus, this test examines the effect of different habitat productivity if we assume PC to be constant. For the same set of scenarios, we further examined the effect of landscape fragmentation by varying H to 0.1 and 0.9.

In a final analysis, we used data from 16 local and regional mammal communities in North America and Australia as input distributions for simulations varying γ_{PI} and SATan. These data comprise five regional communities of typical North American biomes, five communities of homogeneous patches within these biomes (both from Brown and Nicoletto 1991), and six communities of rather heterogeneous regions in Australia (Burbidge and McKenzie 1989). From these data sets we excluded primarily carnivorous and insectivorous, as well as flying species. For each of these communities, the body mass of a component species was drawn with a probability given by a general equation for the body mass scaling of population density in mammals (Damuth 1981a).

1.3.7 Analysis of simulation results and model validation

We validated the model by comparing its predictions to independent data on body mass distributions in animal communities and the scaling relationship between home range size and body mass at the species level. To validate the predicted scaling of home range size, we used results of three empirical studies (Harestad and Bunnell 1979, Holling 1992, Ottaviani et al. 2006). Empirical studies generally agree on a slope of the log-log relationship between body mass and home range size of ~ 1 (see also Haskell et al. 2002, Jetz et al. 2004), whereas the reported intercepts vary substantially. To determine the slopes and intercepts predicted by our model, we analysed the simulation output by fitting ordinary least squares (OLS) regressions to $\log_{10}$-transformed home range size (in ha) versus body mass (in g) in analogy to empirical studies (Holling 1992). OLS regression was used because this is the method employed by all empirical studies used for model validation. Potentially, phylogenetic correlations may cause the species-level allometry of home range size to differ from the individual-level allometry predicted by our model (Pagel and Harvey 1988). However, the only phylogenetically corrected study of home range allometry (Ottaviani et al. 2006) concluded that phylogenetic relatedness has no significant effects. In line with other studies (Haskell et al. 2002, Jetz et al. 2004) we thus assume that the species-level allometries estimated from empirical data also hold at the individual level.

Since there is very little information on the shape of individual size distributions (ISD) in mammal communities (White et al. 2007), we validated the predicted ISD by combining information on the species-level distribution of body mass with information on the relationship between (within-species) population density and body mass. The scaling relationship of population density has been found to have exponents between -0.75 and -1 (Damuth 1981a, Brown et al. 2004, Makarieva et al. 2005, Damuth 2007). In local mammal communities, theory predicts the body mass of species to follow a log-uniform distribution (Brown 1995), which is equivalent to a power law distribution with an exponent of -1. Consequently, one may theoretically expect the distribution of individual body mass to have an exponent between -1.75 and -2. In addition to this theoretical expectation, we obtained 'empirical' lists of individual body mass by combining population density - body mass relationships with exponents of -0.75 and -1 with empirical distributions of species-level body mass in 16 animal communities (Burbidge and McKenzie 1989, Brown and Nicoletto 1991, excluding primarily carnivorous, insectivorous and flying species). To the resulting lists of individual body mass, we then fitted equation 1.1 by means of maximum likelihood optimization. The obtained 'empirical' estimates of the body mass scaling exponent η for the 16 communities range between -1.89 and -1.43, defining an 'empirical' expectation for η (more detailed information is given in Appendix 1.B, Tables 1.B.1, 1.B.2 and 1.B.3). The values of η predicted by our model were similarly obtained by maximum likelihood fitting of equation 1.1 to simulated lists of individual body masses. To evaluate the models we use Nagelkerke-R^2.

While there are some arguments about the shape of the general relationship between body mass and population density in local mammal communities (e.g. Silva and Downing 1995, White et al. 2007), a general pattern seems to be a well defined power law relationship with exponents ranging between -0.75 and -1 above a certain medium body mass of around 100 g (Brown 1995, Silva and Downing 1995, White et al. 2007). Therefore, we additionally compared model output of the basic set of scenarios and validation data only for animals above 100 g. Finally, we also determined the number of individuals in the resulting model communities for comparison with available empirical estimates.

1.4. Results

1.4.1 General patterns of the home range scaling relationship and the body mass distribution

The allometric model produces spatially explicit predictions of home range distribution in heterogeneous resource landscapes (for an example see Fig. 1.2). While home range centres of larger animals are located in the middle of large resource patches, smaller individuals tend to establish home ranges at the periphery of large patches or in smaller patches (Fig. 1.2a). Consequently, the latter regions have a higher overlap of small animal home ranges (Fig. 1.2b).

For a wide range of input distributions and parameters the model produces realistic relationships between home range size and body mass that are well described by allometric power laws (Fig. 1.3a-b). These power laws explain between 38% and 96% of the variance in log-transformed home range sizes.

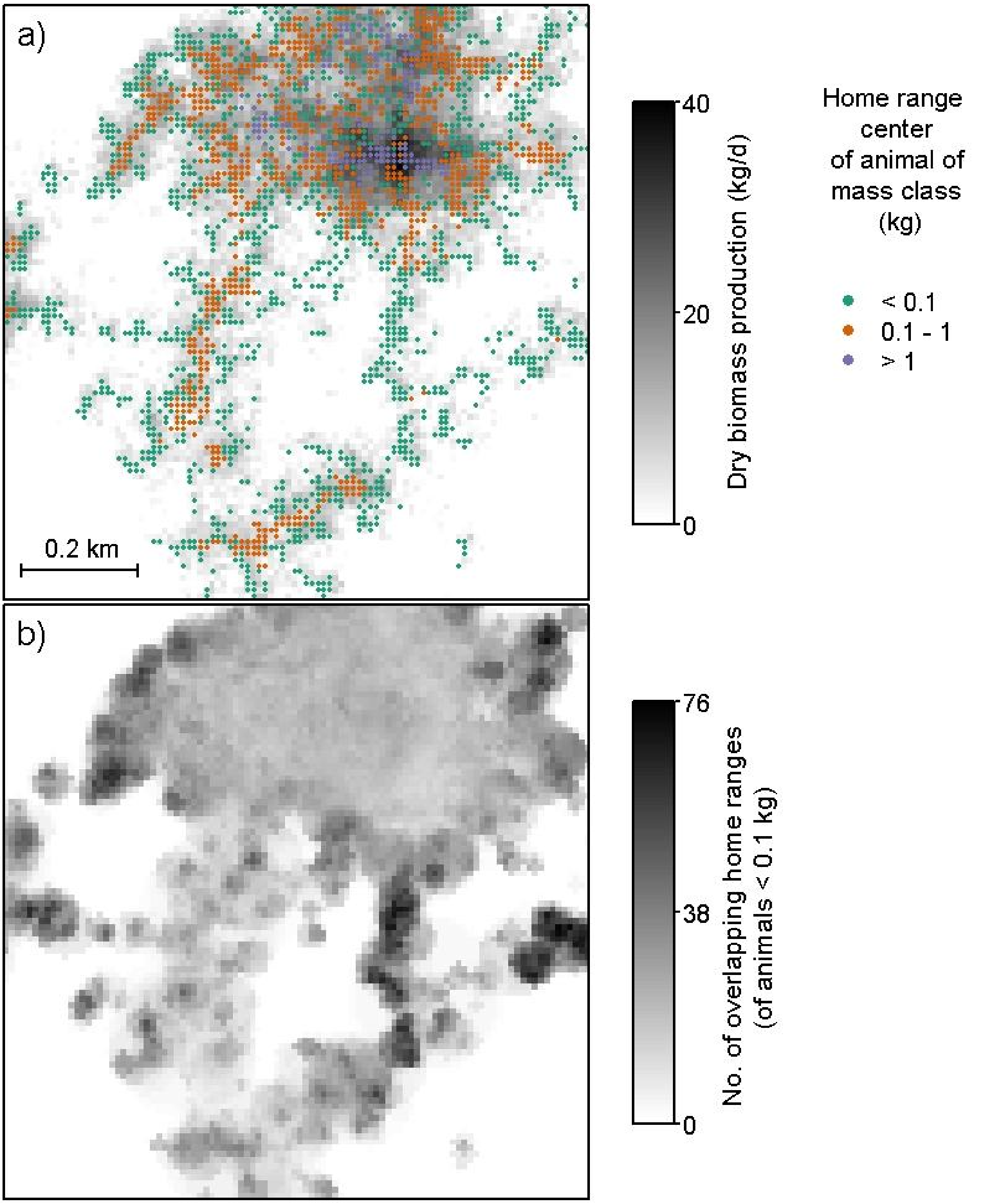

Figure 1.2. Spatial home range patterns in a resource-rich landscape section for one exemplary simulation of the allometric model (power law input distribution with exponent of -1.2, γ_{PL}= 10 × 10^{-2}, SATan = 0.9). a) The central home range cells of three body mass classes are plotted over the resource landscape. b) Spatial variation in home range overlap for the smallest body mass class (< 0.1 kg) in the same landscape section.

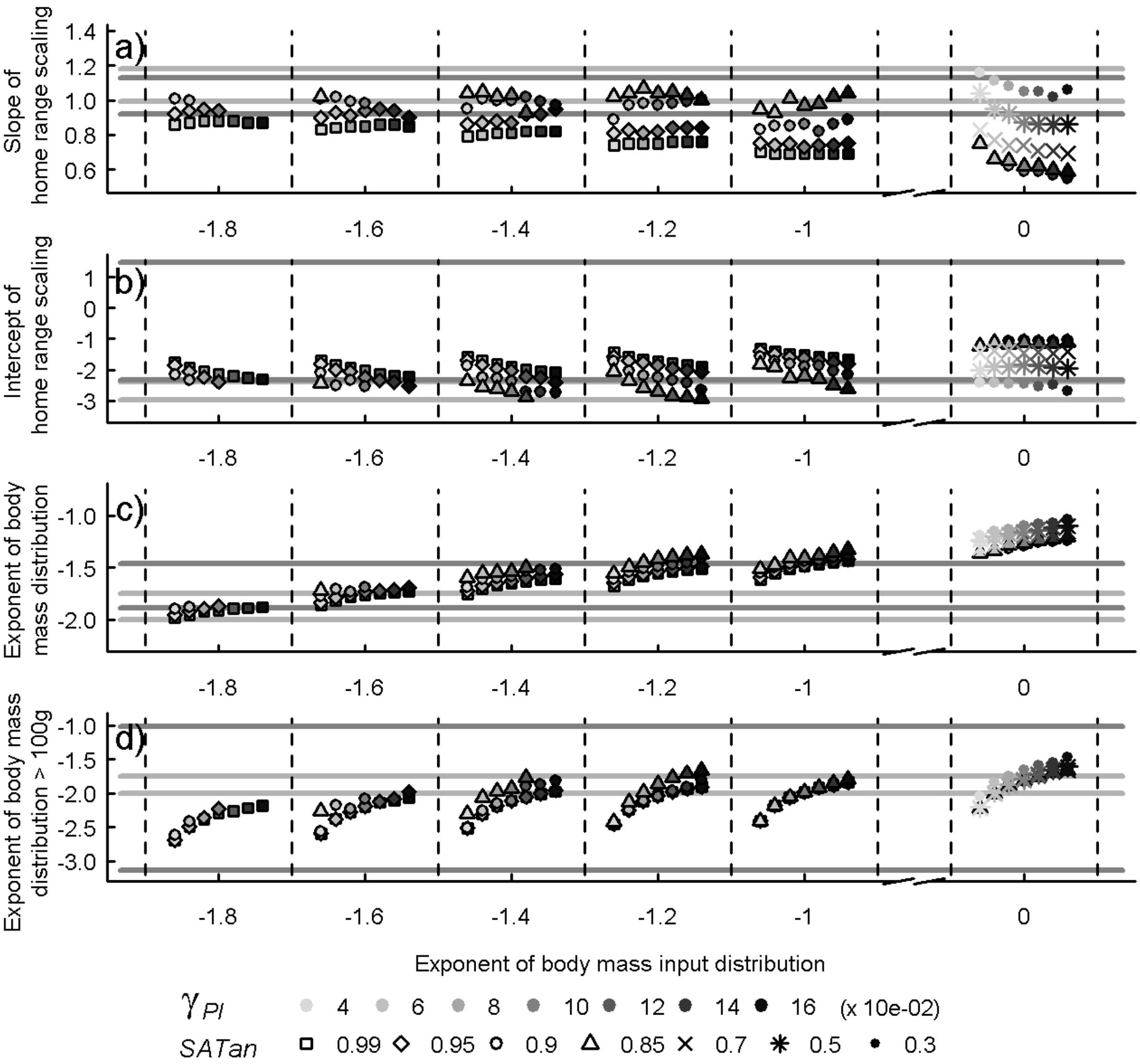

Figure 1.3. Scaling of home range size (a-b) and of individual abundance (ISD) (c-d) with body mass of the modelled mammal community. All results are shown as a function of different body mass input distributions, individual resource use (γ_{PI}) and saturation (SATan). Home range scaling was analyzed by OLS regression of log10-transformed data (body mass in g, home range size in ha). The body mass distribution was analyzed by a maximum likelihood fit. Horizontal lines give value ranges for literature data as validation. For a) and b) light grey lines show the range of data of herbivore mammals, dark grey lines for omnivores (data from Harestad and Bunnell 1979, Holling 1992, Ottaviani et al. 2006, all OLS regression results). For c) and d) light grey lines show the theoretical range of exponents of local communities. Here, dark grey lines indicate the range of results a combination of species data of 16 empirical communities with population density calculation (exponents -0.75 and -1) yielded, using the same analysis as for modelled communities (Methods). Dashed vertical lines separate scenarios with different body mass input distributions.

Low R^2-values arose for very high saturations in combination with steep input distributions. Similarly, the simulated body mass distributions were fit well by power law distributions (Nagelkerke-R^2 was always > 0.98). Variability between landscape replicates was fairly low (e.g. the absolute coefficient of variation was consistently < 0.1 and < 0.033, for scaling exponent of home range size and individual abundance, respectively).

For all but the highest landscape saturation levels (i.e. SATan = 0.99), the majority of scenarios with power law body mass input distributions steeper than -1 agree well with empirical data. The modelled communities of these scenarios are in line with empirical findings regarding home range scaling relationships as well as regarding the range of exponents of the body mass distributions if the body mass distribution is analysed over the whole range of body masses (Fig. 1.3a-c). Generally, lower saturation levels yield realistic home range scaling for scenarios with less steep input distributions (Fig. 1.3a). These scenarios, however, result in model communities with less steep body mass distributions compared to validation communities (Fig. 1.3c). The number of animals in the community is within reasonable ranges (13516 ± 1430 on 1 km^2 of suitable habitat; mean ± 95% C.I.; comparable validation data are given in Table 1.B.3).

Body mass distributions of all scenarios show a higher scaling exponent if data are fitted beyond a body mass of 100 g and the difference between scaling exponents of scenarios with different input distributions decreases (Fig. 1.3d). Above 100 g also scenarios with uniform body mass input distribution yield realistic body mass distributions.

Individual resource use (γ_{PI}) has little influence on the exponent of home range scaling for scenarios with steep input distributions (Fig. 1.3a). Increased γ_{PI}, however, leads to decreasing home range sizes of all animals (i.e. reduces the intercept of the home range allometry) (Fig. 1.3b), and to less steep body mass distributions (i.e. shifts the community composition towards more large animals) (Fig. 1.3c). For scenarios with uniform input distribution higher γ_{PI} decreases the slope rather than the intercept of home range scaling. Saturation shows consistent effects for all scenarios. Lower SATan (i.e. less dense animal packing) increases the slope and decreases the intercept of home range scaling while increasing the scaling exponent of the body mass distribution (Fig. 1.3a-c).

To examine the mechanisms shaping home range allometries in more detail, we conducted additional simulations in which we varied locomotion costs (from 0% to 100% of the standard costs) and saturation (from 0.825 to 0.925) for the scenario depicted in figure 1.2. We found that the home range slope of small animals (< 1 kg) is shaped by saturation but not locomotion costs ($F_{1,27} = 87.21$, $p < 0.01$ and $F_{1,27} = 0.30$, $p = 0.59$). In contrast, the home range slope of large animals (≥ 1 kg) is affected by locomotion costs but not saturation ($F_{1,27} = 24.22$, $p < 0.001$ and $F_{1,27} = 2.28$, $p = 0.14$).

The model's ability to decrease the scaling exponent and hence to 'shape' the community body mass distribution, varies with the body mass input distribution (Fig. 1.4). The model affects shallower input distributions more strongly than already steep input distributions. Figure 1.4 even suggests a non-linear relationship between this 'steepening effect' of the model and the slope of the input distribution.

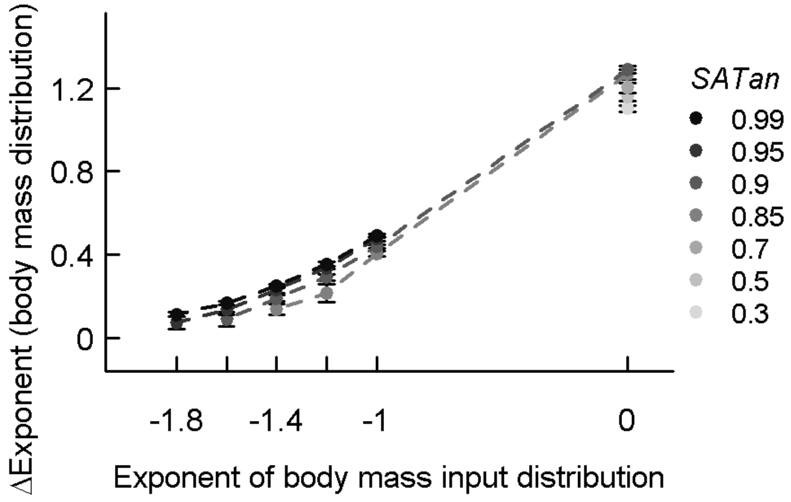

Figure 1.4. Effect the simulation model has on shaping the body mass distribution of the mammal community in dependence of the body mass input distribution. Values are the difference between the exponent of the body mass input distribution and the resulting body mass distribution. Results are shown exemplarily for different scenarios with γ_{PI} of 10×10^{-2}. Shades of grey indicate saturation levels. Error bars are 95% C.I.s of the five landscape replicates of each scenario. Note that not all saturation levels could be achieved for all scenarios; for reasons see Appendix 1.A.

The use of sixteen different empirical body mass input distributions from North America and Australia results in similar patterns regarding home range scaling and the shape of the community body mass distribution as the theoretical input distributions (compare Fig. 1.3 and 1.5). Again, all but the highest levels of saturation (i.e. SATan = 0.99) result in model communities that agree with validation data, regarding home range scaling as well as the exponent of the body mass distribution of local communities (Fig. 1.5a-c).

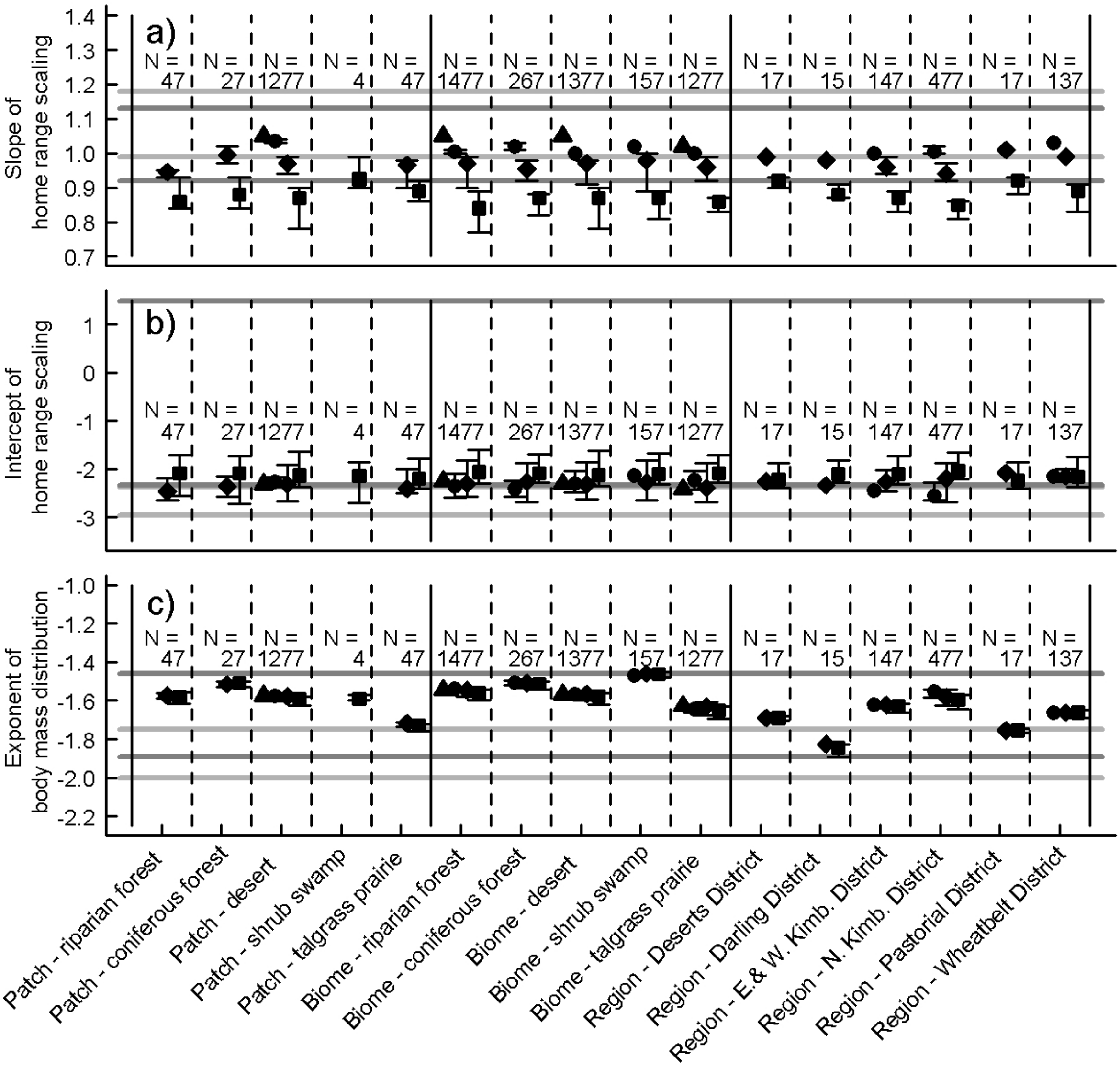

Figure 1.5. Simulation results of scenarios with empirical communities of different habitat types and different spatial scales as input distributions. These were achieved by combining, species data with an allometric relationship of population density (Methods). Symbols indicate saturation (square: SATan = 0.99, diamond: SATan = 0.95, circle: SATan = 0.9, triangle: SATan = 0.85). They show the median, error bars show the range of results of scenarios that differed in γ_{PI} (varied from 4 to 16×10^{-2} in steps of 2×10^{-2}). Labels show the number of scenarios that are described by each symbol/error bar. Horizontal lines give the range of validation data (details in Fig. 1.3). Dashed vertical lines separate scenarios with different body mass input distributions (dashed lines for different scenarios within one local scale, solid lines for different local scales). Note that here, due to the discrete input distributions, saturation is reached very quickly. This leads to exclusion of various scenarios with lower saturations by only considering scenarios with CFA > 2 (see Appendix 1.A).

1.4.2 Effects of community resource availability and landscape heterogeneity

The model proves to be reasonably robust against changes in habitat productivity, implemented as change in resource supply to the community (PC × R). If these resources are doubled or halved, resulting home range scaling parameters as well as the exponent of the community body mass distribution are still within the range of validation data (Fig. 1.6a-c).

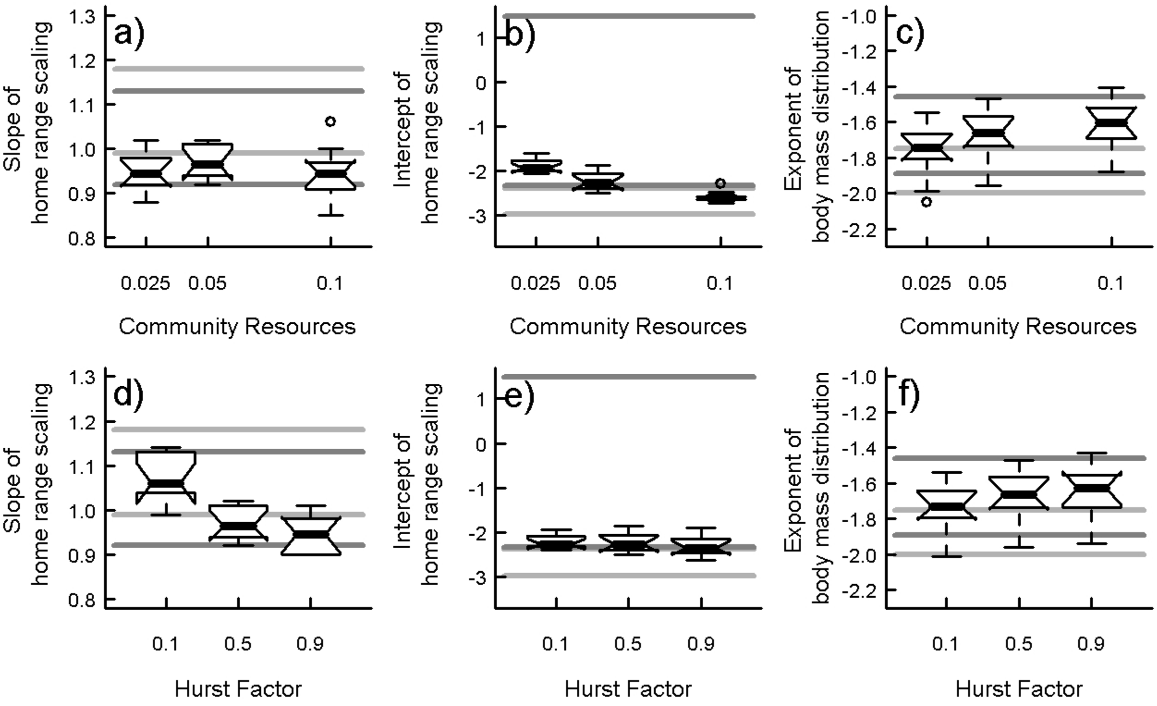

Figure 1.6. Test of the effects of changed resource production that is available to the community (PC × R) in kg × m^{-2} × $year^{-1}$, and of the effect of changing heterogeneity of the landscape, i.e. the clumpiness of resources (Hurst-factor of 0.1 for strongly fragmented, 0.9 for strongly clumped resource distributions). Varying community resources either represents a systematic change of PC, the fraction of resources the mammal community can use, or variation of the productivity of the habitat if PC is assumed to be constant. Simulation experiments shown in this figure were done for a random selection of 10 of those scenarios, shown in figure 1.2, yielding realistic results for all four target values. Box plots show median, 25% and 75%-quantiles; whiskers indicate the range of values, notches give 95% C.I.s of the median, and small circles show outliers. Horizontal lines give the range of validation data. For details see caption of figure 1.2.

Landscape and resource fragmentation rather strongly affect the slope of the home range allometry: strongly heterogeneous landscapes result in steeper home range scaling (Fig. 1.6d), which, however, still remains within the range of reported values. The intercept as well as the body mass distribution are less influenced by fragmented resource distribution (Fig. 1.6e-f).

1.5 Discussion

This study is to our knowledge the first that derives spatial and compositional community patterns in heterogeneous resource landscapes from individual physiology and behaviour. This is successfully done by combining an allometric approach for describing physiological properties of different individuals with an individual-based model of home range formation. While the role of resources for the structure and composition of animal communities has been controversially discussed for many years (Damuth 1981a, Richie and Olff 1999, Carbone et al. 2007, Damuth 2007), our approach represents a new way to understand such communities via the spatial requirements of competing individuals, derived from resource needs and resource use characteristics given realistic resource distributions (Fig. 1.1). The presented model predicts spatially explicit distributions of home ranges in animal communities (Fig. 1.2). Moreover, it predicts both realistic home range size - body mass relationships and realistic distributions of individual body mass (Fig. 1.3), two highly complex and yet mainly independently investigated patterns characterizing terrestrial communities. These predictions are largely robust to variation in parameter values, input distributions, habitat productivity and landscape fragmentation (Fig. 1.3, 1.5 and 1.6). If the body mass distribution is restricted to the range above 100 g for which there seems to be a better agreement about the body mass scaling of population density (Brown 1995, Silva and Downing 1995, White et al. 2007), an even wider parameter range generates realistic exponents of body mass distribution (Fig. 1.3d). Moreover, the model also yields realistic prediction when applied to specific communities (Fig. 1.5).

1.5.1 Mechanisms and model behaviour

The response of the model output variables to changing levels of individual resource use (γ_{PI}) and saturation (SATan) (Fig. 1.3) reflect the underlying mechanisms of home range formation. Increased resource availability (γ_{PI}) results in smaller home ranges since the resource requirements of all individuals can be fulfilled on smaller areas. This should lower the intercept of the home range allometry, as is the case for steep input distributions (Fig. 1.3b). High resource availability also facilitates the establishment of large animals which makes body mass distributions more shallow (Fig. 1.3c-d). This particularly holds for uniform input distributions for which large animals have a higher probability to get selected. However, for uniform input distributions increasing resource availability also reduces the slope of the home range allometry. This is because the home range sizes of the largest animals (which are favoured by increased resources) are strongly limited by the high (allometric) locomotion costs in the patchy resource landscape (as indicated by the regression analysis of factors controlling home range allometry). Thus, the realised home ranges of the largest animals are at the lower end of the theoretically possible size spectrum.

As a consequence, increasing resource availability lowers the slope of the home range scaling while the corresponding intercept remains largely unchanged (Fig. 1.3b).

Lower saturation (SATan) means that the rather small and unfavourable potential home ranges in areas where the resource level is already reduced by other animals are not yet occupied. As saturation increases these marginal areas are predominantly occupied by small animals because they cannot fulfill the resource requirements of large animals. However, since resource levels are already low, the resulting home ranges of small animals are comparatively large. Therefore higher saturation results in i) shallower slopes of the home range allometry (due to larger home range size of small individuals, Fig. 1.3a), ii) larger intercepts (due to generally larger home ranges when resource levels are reduced, Fig. 1.3b), and iii) a steeper body mass distribution (due to a higher proportion of small animals, Fig. 1.3c-d).

This behaviour of our model matches well with optimal foraging theory and the home range concept (Mitchell and Powell 2004). The fact that the model also produces realistic community patterns suggests that allometry, resource competition and optimal foraging have pronounced effects on community structure.

1.5.2 Body mass input distribution and community saturation

The body mass input distribution was found to affect the resulting community composition. If the input distribution is interpreted as the pool of dispersers entering the local community from the regional metacommunity, this raises questions about processes structuring regional species pools and local communities. Understanding how metacommunity dynamics and specific animal traits (like body mass) affect colonization and local community assembly still poses a great challenge to ecologists (compare Starzomsky et al. 2008).

Our simplistic model only contains the mechanisms that are believed to be most relevant in structuring communities at the local scale (Said and Servanty 2005, Allen et al. 2006, Starzomsky et al. 2008). Other processes that probably also affect the body mass distribution of communities include the evolution of physiological properties (Brown 1995, Clauset and Erwin 2008), as well as biogeographical factors and dispersal ability (Allen et al. 2006). While these processes and factors typically affect the relationship between species richness and body mass on rather large temporal and spatial scales, they can also have a direct impact on population density (for evolutionary processes affecting population density see Damuth 2007). At local scales also processes other than resource competition, which is explicitly included in our model, can shape community patterns. Amongst these processes are population dynamics affected by environmental variation (McLeod 1997), disturbances and environmental stress (Makarieva et al. 2005), or predation pressure (Stanford 1995). Also community age or assembly time can play a major role for community structure and composition (Starzomski et al. 2008).

Some of the factors and processes that are not explicitly described in the model might be subsumed by two rather integrative ‘parameters’: input distribution subsumes processes acting at larger scales, whereas saturation may stand for unresolved processes acting at the local scale. Low saturation might result from short assembly times (Mouquet et al. 2003, Starzomski et al. 2008), strong or frequent disturbances (Makarieva et al. 2005) or high predation pressure. These processes seem particularly important under shallow input distributions for which realistic community structure is obtained with relatively low saturation levels (Fig. 1.3). In contrast, for steep input distributions community structure is dominated by regional mechanisms shaping the input distribution (Fig. 1.4) and not by local mechanisms that are modelled explicitly or subsumed in the saturation parameter.

The two integrative parameters (saturation and input distribution) also help to interpret our non-dynamic model in a dynamic context. In a dynamic context, the processes explicitly incorporated in our model should favour small animals. For example, with steep input distributions any resource patch freed by the death of a large animal is likely to be occupied by a smaller rather than a larger animal. Over the course of time this would lead to a disappearance of large animals. Yet, in our non-dynamic model, low saturation (which leads to a shallower body mass distribution) may implicitly mimic local scale mechanisms that privilege large animals, such as lower vulnerability to disturbance or predation, more successful home range defence, or longer life spans. Similarly, shallow input distributions implicitly represent mechanisms that favour large animals at the regional (or metacommunity) scale, for example their higher dispersal capacity (Etienne and Olff 2004).

1.5.3 Landscape heterogeneity and resource availability

Strikingly, model results were robust and in good agreement with empirical data for a broad range of landscape fragmentation levels. Model response to resource fragmentation is realistic considering optimal foraging principles. Steeper home range scaling when resources are strongly scattered results out of the need for bigger feeding areas, particularly for larger animals. However other behavioural aspects such as altered foraging behaviour or avoidance in face of crowding in remaining habitat patches, leading to a different response of home range size, might be also important in real systems (Banks et al. 2007).

The model is also robust against variation of resource supply to the community, which can for example represent different types of habitats. For a wide range of parameter values the model makes realistic predictions when resource levels are changed. Community response regarding home range sizes also is in line with optimal foraging principles. The general robustness of home range scaling agrees with reported observations of relatively constant home ranges across habitats

(Orland and Kelt 2007) and the interpretation of home ranges as ecological footprint of a species (Makarieva et al. 2005).

1.5.4 Model limitations and possible extensions

The simple mechanistic approach taken here obviously ignores several factors and processes that may shape home range distributions and communities, for example predation, mutualism and parasitism (Wootton 1994, Stachowicz 2001), indirect effects via interactions with other species (Wootton 1994), or intraspecific genetic variation (Agrawal 2004). Given these omissions, it is even more striking that the model predictions for a range of scenarios agree well with empirical data on home range scaling and biomass distribution. Clearly the model could be extended to incorporate other factors such as territoriality or use of multiple resources. Territoriality could be modelled by increasing the depletion of resources within the home range of territorial animals while imposing certain costs. Use of multiple resources could be integrated into the model by varying the availability or use of different resources, i.e. the niche position along a resource gradient, as a function of an animal's body mass (compare Carbone et al. 2007). Such simulations could elaborate the influence of niche width and niche overlap on community composition. The integration of population dynamics and disturbance would help to assess how these processes interact with individual resource use in shaping community structure. More accurate description of movement patterns implying locomotion costs in regard of home range establishment would help to get a more detailed understanding of individual in situ resource use in light of competition and its relation to home range. Other patterns that could be further explored with our model comprise various aspects of the spatial distribution of animals, for example home range overlap and its dependence on body mass and resource distributions, detailed measures of assembly history, or – in the case of simulations with explicit species identity – the relative contribution of inter- and intraspecific competition. Such extensions and refinements would help to test and validate our findings.

1.5.5 Implications for empirical research

Our model is based on empirically measured allometric relationships for feeding rate and movement costs. In addition to these established allometric relationships, the model requires quantitative information on the spatial distribution of resources, the saturation of the animal community, foraging behavior and resource use by individuals. Data on spatial resource distributions can be obtained through the combination of remote sensing techniques with field measurements. Saturation, as another factor that we found to have a role in structuring animal communities, could be determined empirically as the percentage of resources not consumed by the entire community. More refined descriptions of individual foraging behaviour and locomotion costs are likely to arise from the rapidly developing field of movement ecology (Nathan et al. 2008). In particular technical developments in biotelemetry (e.g. Wilson et al. 2008) combined with novel mechanistic modelling approaches (Van Moorter et al. 2009) will improve our understanding of different aspects of individual movement in heterogeneous landscapes. Recent advances in biotelemetry may also enable the quantification of the ‘per capita share of community resources’ (PI) as a key parameter of our model. In this respect, the use of miniature data loggers that continuously record the physiology and environment of free-ranging animals in the wild (Wilson et al. 2008) seems particularly promising. Clearly, the direct quantification of some model parameters still poses practical challenges. However, by identifying key parameters relevant for the spatial structure of animal communities, our model provides guidance for future empirical research on this subject.

Novel data useful for testing the spatially explicit and individual-based predictions of our model may emerge from future trait-based studies of animal communities (McGill et al. 2006). Such studies may produce data on the assembly history of communities, the competition structure in assemblages and the spatial distribution of individual home ranges in communities. Finally, it seems important to conduct allometric studies of home range size and abundance at the individual level and to control for phylogenetic relatedness in species-level allometric analyses (Pagel and Harvey 1988, Ottaviani et al. 2006).

1.6 Conclusion

In a recent review on key gaps in population and community ecology, Agrawal et al. (2007) conclude that modern community ecology is poised to move beyond lists of community-structuring factors to a predictive framework of how factors interact to shape communities. Our bottom-up model provides such a mechanistic framework that helps to understand and predict structural patterns (home range distribution and body mass distribution) of animal communities in fragmented landscapes. The good agreement with validation data for most model scenarios emphasizes the importance of spatial processes for community structure and indicates the linkage between its spatial and compositional patterns. This simple mechanistic model helps us to understand how individual behaviour and interactions scale up to community composition and structure and identifies key challenges for future empirical research on spatial resource use in animal communities. Furthermore, the spatial modelling concept allows further and more accurate investigation of spatial factors, such as landscape fragmentation or habitat loss, on community structure. The tight linkage of simple mechanistic models to creative experiments, observational studies and comparative analyses becomes increasingly important as ecologists try to understand and mitigate the impacts of environmental changes on communities.

1.7 Appendix 1.A - Calculation of system saturation and definition of scenarios

In this appendix we explain how the termination criterion CFA, consecutively failing animals before simulation stops, is related to system saturation.

The effect of CFA was always analysed in steps of 2 units from 0 to 5,000 for rapidly saturating scenarios with power law body mass input distribution, and in steps of 20 units from 0 to 50,000 for slowly saturating scenarios with uniform input distribution; separately for each of the 5 replicates. The maximum values of CFA were chosen to avoid extremely long computing times without anymore significant changes (see Fig. 1.A.1). A simple and direct community measure, the number of individuals, shows a clear saturation effect with increasing CFA.

The saturation level of the total number of animals NoAn was estimated by fitting a Michaelis-Menten kinetics saturation curve (Monod function) using non-linear least squares regression (Gauss-Newton algorithm)

$$\mathrm{NoAn} = \frac{\mathrm{a} \times \mathrm{CFA}}{\mathrm{b} \times \mathrm{CFA}} \,. \qquad (1.\mathrm{A}.1)$$

For scenarios with uniform input distribution the model fitted the data perfectly. For scenarios with other power law input distributions the curve showed very fast saturation. By only considering NoAn-values > 0.8 × NoAn (CFA = 5,000) for the fit we also achieved very good agreement between model and data for these scenarios (Fig. 1.A.1); lower saturations were not considered for these scenarios anyway for reasons of stochasticity, see below.

We then can calculate a saturation level in terms of animal numbers or community-level carrying capacity

$$\mathrm{SATan} = \frac{\mathrm{NoAn}}{\mathrm{a}} \,, \qquad (1.\mathrm{A}.2)$$

where a is the asymptote of the saturation curve and so the number of successful animals the model predicts at complete saturation.

For a defined series of SATan-values (between 0.3 and 0.99) the corresponding CFA was then derived for each scenario in order to be used as equivalent termination criterion for simulations. A specific combination of parameters (resource availability to community and individuals and the input distribution) and one specific level of saturation (SATan) are regarded as a scenario. We only analysed scenarios with a corresponding CFA within the range used for the saturation fit (i.e. up to 5,000 or 50,000, dependent on the choice of input distribution). When steep input distributions were used saturation was reached at extremely low CFA and the stochastic effect of the input distribution then dominated simulation results at low saturation. We therefore discarded scenarios with CFA < 3 to eliminate most of this stochastic effect and guarantee comparability between different scenarios.

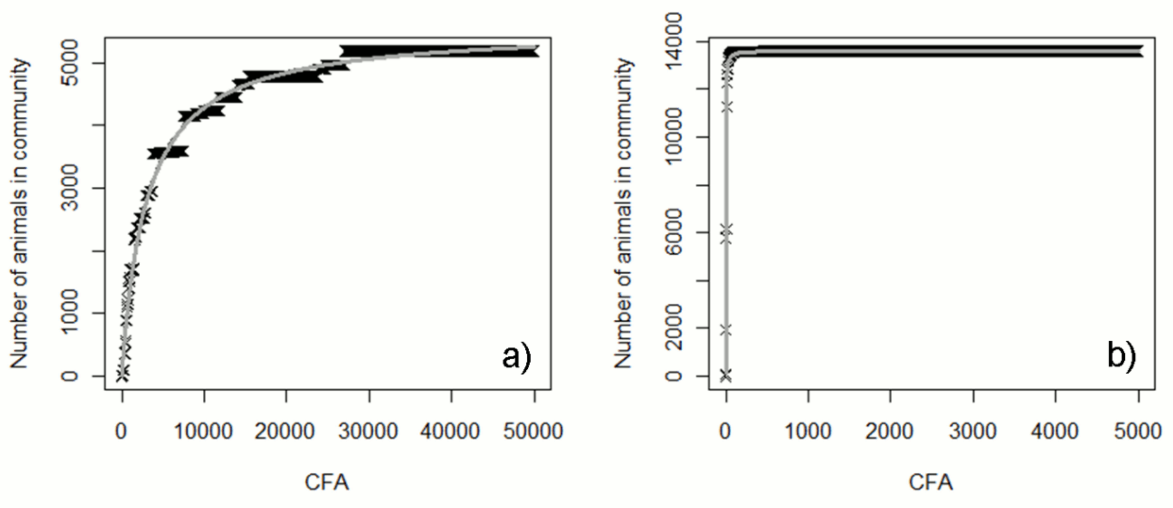

Figure 1.A.1. Illustration of the relationship between number of animals in the community and CFA, the number of consecutively failing animals used as a termination condition for the simulations. One replicate of a simulation with uniform input distribution (a) and one with power law input distribution (exponent -1.2) (b) is shown, both with γ_{PI} of 10 × 10^{-2}. The light grey line shows the fitted Monod model.

1.8 Appendix 1.B – Analysis of validation data

Table 1.B.1. Analysis of validation data for the scaling exponent of species richness and individual abundance by a maximum likelihood fit of a power law probability density function.

	Species no.			Individual no.		
	Min. exponent	Max. exponent	Mean exponent	Min. exponent	Max. exponent	Mean exponent
Patch (n=5)	-1.23	-1.03	-1.09	-1.79	-1.46	-1.59
Biome (n=5)	-1.15	-1.06	-1.11	-1.71	-1.43	-1.54
Region (n=6)	-1.08	-1.02	-1.05	-1.89	-1.51	-1.68
Overall (n=16)	-1.23	-1.02	-1.08	-1.89	-1.43	-1.61

Fits from 5 g to 100 kg (the body mass range in the model); only species within this range were considered. Species data for 5 different North American biomes (riparian forest, coniferous forest, desert, shrub swamp, and talgrass prairie) and of 5 homogeneous patches within these biomes from Brown and Nicoletto (1991); species data for 6 different rather heterogeneous regions in Australia from Burbidge and McKenzie (1989); primarily insectivorous and carnivorous as well as aerial species were excluded before analysis. Relative number of individuals for the fit of individual abundance was calculated for each species by applying allometric equations for population density with exponents of -0.75 and -1 to all communities; Shown results are summaries from all these different fits.

Table 1.B.2. Analysis of validation data for the scaling exponent of species richness and individual abundance by a maximum likelihood fit of a power law probability density function. Only species with body mass > 100 g are considered for this analysis.

	Species no.			Individual no.		
	Min. exponent	Max. exponent	Mean exponent	Min. exponent	Max. exponent	Mean exponent
Patch (n=5)	-1.21	-0.92	-1.09	-3.14	-1.15	-1.99
Biome (n=5)	-1.31	-1.12	-1.20	-2.45	-1.70	-2.08
Region (n=6)	-1.21	-0.77	-1.01	-2.58	-1.02	-1.95
Overall (n=16)	-1.31	-0.77	-1.10	-3.14	-1.02	-2.00

Fits from 100 g to 100 kg; only species within this range were considered. Species data for 5 different North American biomes (riparian forest, coniferous forest, desert, shrub swamp, and talgrass prairie) and of 5 homogeneous patches within these biomes from Brown and Nicoletto (1991); species data for 6 different rather heterogeneous regions in Australia from Burbidge and McKenzie (1989); primarily insectivorous and carnivorous as well as aerial species were excluded before analysis. Relative number of individuals for the fit of individual abundance was calculated for each species by applying allometric equations for population density with exponents of -0.75 and -1 to all communities; Shown results are summaries from all these different fits.

Table 1.B.3. Number of species and individuals in validation communities.

	Species no.			Individual no.		
	Min. no.	Max. no.	Mean no.	Min. no.	Max. no.	Mean no.
Patch (n=5)	16	22	19.0	9455	21153	13742
Biome (n=5)	40	86	65.6	21918	64258	44635
Region (n=6)	9	24	16.7	7687	16653	11580
Overall (n=16)	9	86	32.7	7687	64258	22585

Values given are for species with a body mass between 5 g and 100 kg. Species data for 5 different North American biomes (riparian forest, coniferous forest, desert, shrub swamp, and talgrass prairie) and of 5 homogeneous patches within these biomes from Brown and Nicoletto (1991); data for 6 different rather heterogeneous regions in Australia from Burbidge and McKenzie (1989); primarily insectivorous and carnivorous as well as aerial species were excluded before analysis. Number of individuals is per km² and was calculated for each species by applying a reported allometric equation for population density after Damuth (1981a) for mammals.

Link to the next chapter

In Chapter 1 I introduced a new allometric modelling approach that simulates mammal communities on the basis of individual home range formation in spatially explicit resource landscapes. The search and the establishment of individual home ranges integrate animal physiology and behaviour as well as intra- and interspecific competition. Therefore the new mechanistic model of home range formation in animal communities can be perfectly applied to explore the role of the different mechanisms involved in structuring communities. In addition to the movement approach already used in Chapter 1 (based on an approach originally introduced by Mitchell and Powell 2004), in Chapter 2 two new movement models are introduced which represent fundamentally different foraging strategies. The three strategies, namely a 'central place forager', a 'patrolling forager' and a 'body mass dependent nomadic forager', are tested for their efficiency for animals of different body sizes, followed by a thorough elaboration of how this will in turn affect community structure and community response to habitat loss.

Chapter 2

Movement upscaled – the role of individual foraging movement for community response to habitat loss

---

A version of this chapter is published as: Buchmann, C. M., Schurr, F. M., Nathan, R. and Jeltsch, F. (2011) Movement upscaled – the importance of individual foraging movement for community response to habitat loss. *Ecography*, **34**, 001-010.

2.1 Abstract

Habitat loss poses a severe threat to biodiversity. While many studies yield valuable information on how specific species cope with such environmental modification, the mechanistic understanding of how interacting species or whole communities are affected by habitat loss is still poor. Individual movement plays a crucial role for the space use characteristics of species, since it determines how individuals perceive and use their heterogeneous environment. At the community level, it is therefore essential to include individual movement and how it is influenced by resource sharing into the investigation of consequences of habitat loss. To elucidate the effects of foraging movement on communities in face of habitat loss, we here apply a recently published spatially explicit and individual-based model of home range formation. This approach allows predicting the individual size distribution (ISD) of mammal communities in simulation landscapes that vary in the amount of suitable habitat. We apply three fundamentally different foraging movement approaches (central place forager (CPF), patrolling forager (PF) and body mass dependent nomadic forager (BNF)). Results show that the efficiency of the different foraging strategies depends on body mass, which again affects community structure in face of habitat loss. CPF is only efficient for small animals, and therefore yields steep ISD exponents on which habitat loss has little effect (due to a movement limitation of body mass). PF and particularly BNF are more efficient for larger animals, resulting in less steep ISDs with higher mass maxima, both showing a threshold behaviour with regard to loss of suitable habitat. These findings represent a new way of explaining observed 'extinction thresholds', and therefore indicate the importance of individual space use characterized by physiology and behaviour, i.e. foraging movement, for communities and their response to habitat loss. Findings also indicate the necessity to incorporate the crucial role of movement into future conservation efforts of terrestrial communities.

2.2 Introduction

Though it is well documented that habitat loss and increasing landscape fragmentation are responsible for an ongoing loss of biodiversity (Andren 1994, Harrison and Bruna 1999, Ewers and Didham 2006), we still lack a mechanistic understanding of how interacting animal communities respond to these landscape alterations. For several terrestrial animal species, empirical studies provide valuable knowledge about the response of single species to landscape modifications, with respect to abundance and distribution, but also social and behavioural aspects (e.g. Bowers et al. 1996b, Said and Servanty 2005, Norris et al. 2010). While some studies refer to such investigations to draw generalizations and conclusions for communities as well (Fahrig 2003, Ewers and Didham 2006), the necessary next step to simultaneously address complete communities is largely missing. In this context, individual movement plays a crucial role, because it determines how individuals perceive and manage to cope with heterogeneous environments (Nonaka and Holme 2007). As movement controls to which subset of the environmental variation in the landscape animals are exposed, it also affects competition between individuals and can be seen as a bridge between behaviour, landscape ecology and population dynamics (Morales et al. 2010).

More and more studies in recent years deal with different aspects of animal movement (e.g. movement decisions and movement modes), their relation to population dynamics and demography and the interplay with landscape properties (Aars et al. 1999, Russel et al. 2003, Rhodes et al. 2005, Romero et al. 2009, Leblond et al. 2010). Different models were developed for explaining and understanding individual movement paths or space use patterns (for reviews see Börger et al. 2008, Patterson et al. 2008, Schick et al. 2008, Owen-Smith et al. 2010). While the investigation of how movement affects populations is a field of active research (see references above and Nathan et al. 2008 as well as Morales et al. 2010), the consequences of movement for communities of interacting individuals of different species are largely unexplored.

In a recent approach Buchmann et al. (2011a) introduced a novel allometric, individual-based modelling approach which allows predicting community structure in an explicit landscape context by simulating individual home range formation of an entire mammal community in a spatially explict way. Thus, this approach scales from individual physiological properties and foraging behaviour to complex community patterns and can be used to explore the effects of landscape structure on communities.

Evidently, different movement strategies and foraging modes affect the space use characteristics of species (Swihart et al. 1988, McLaughlin 1989, Benhamou 1996) and will therefore be responsible for how communities react to habitat loss. To give an example, a community of central place foraging species or other species with a strong focus on one point of attraction (e.g. a nest with offspring) depends on a high habitat quality close to these focal points (compare Mitchell and Powell 2004, Rhodes et al. 2005). Therefore, one can expect such communities to show a different response to changes in landscape configuration than communities composed of species that, for example, have a more patrolling foraging pattern. These 'patrolling foragers' do not need to return over and over again to a specific location in their home range but forage during longer forage bouts, still patrolling the complete home range every day. Animals which behave in a nomadic way within their home ranges, i.e. they only forage in different subsets of the home range over time, can be seen as a further special case. Such 'nomadic foragers' will be even less constrained with respect to their movement decisions, which in turn will affect individual space use characteristics and hence community structure.

In this paper we apply the spatially explicit and allometric model of community structure by Buchmann et al. (2011a) in order to test for the first time the response of the body mass distribution (namely the individual size distribution (ISD) after White et al. 2007) of a mammal community to habitat loss. We use ISD as a distinctive community feature that characterizes community responses to habitat changes. To investigate the effect of foraging movement on community structure as well as its effect on the response of the community to habitat loss, three fundamentally different movement approaches are used within the modelling framework. These foraging movement models span the range from a centred foraging mode over foraging while patrolling the home range to more nomadic foraging movement behaviour.

2.3 Methods

Our modelling framework simulates community assembly and aims at testing for the effect of individual foraging movement on community structure and how this movement affects the response of communities to habitat loss. In the following section, we first describe the generation of the simulation landscapes and habitat loss. Secondly, we briefly explain the allometric and individual-based model of home range establishment and how it is used to simulate the assembly of animal communities (further model details are given in Buchmann et al. 2011a and in Appendix 2.A, which provides a model description following the standard ODD protocol (Grimm et al. 2010)). We then go into more detail about how 3 different foraging movement approaches ('central place forager – CPF', 'patrolling forager – PF', and 'body mass dependent nomadic forager' – BNF) are incorporated in this modelling framework.

2.3.1 Landscape generation

The well established midpoint displacement algorithm (Saupe 1988, Hargrove et al. 2002, Körner and Jeltsch 2008) was used to generate realistic three-dimensional fractal landscapes that are characterized by two parameters: the Hurst-factor H (determining spatial autocorrelation) and σ^2

(variance in displacement of points). The z-values of the landscape grid are interpreted as resource productivity. The landscapes used in simulations have an extent of 257 × 257 grid cells, with each cell being interpreted as 10 × 10 m (i.e. landscapes of ~ 6.6 km^2). For all simulations we used moderate autocorrelation (H = 0.5) and variance (σ^2 = 30) (Fig. 2.1), i.e. the level of landscape fragmentation remained unchanged across habitat loss scenarios (for analyses on effects of landscape fragmentation without habitat loss see Buchmann et al. 2011a).

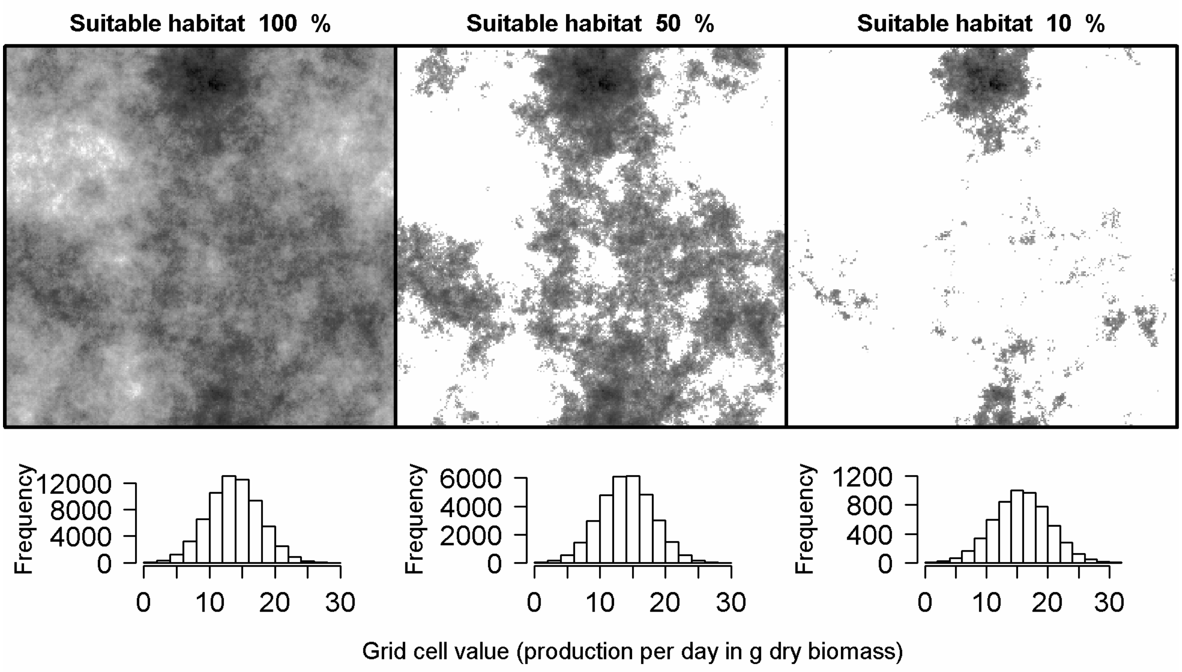

Figure 2.1. Two-dimensional illustration of fractal simulation landscapes (257 × 257 grid cells). Grey scale values show the daily resource production in a cell (from light grey to black, corresponding to ~ 0.1 to ~ 30 g dry biomass, respectively). The landscapes (suitable area 100%) were 'flooded' (i.e. setting the cells with low resource values to 0) until a certain amount of cells were left as suitable cells. Subsequently, these resource landscapes were re-scaled to ensure that suitable cells in all habitat loss scenarios have the same relative frequency of resource production.

To investigate habitat loss effects, these landscapes were then 'flooded' by setting the lowest grid cell suitability values to 0 until a certain amount of productive (suitable) habitat was left (Fig. 2.1). We tested shares of suitable area of 1.0 ('non-flooded'), 0.75, 0.5, 0.3, 0.1 and 0.05. To assure that all simulation landscapes have a comparable range of productivity values, these 'flooded' landscapes were rescaled, using a rank-based transformation, according to the normal distribution of cell values of the 'non-flooded' landscape (in order to have the same mean and the same standard deviation of grid cell values). After rescaling, productive cells in all landscapes had an average productivity of 6.85 × 10^{-2} kg dry biomass × grid cell^{-1} × day^{-1}, oriented towards the productivity of typical shrub lands and grasslands (Whittaker 1975). We assume that 20% of this productivity is available to the mammal community, while the remainder is either not consumable or is lost to other taxonomic groups (see Buchmann et al. 2011a for analyses of the effects of landscape fragmentation and the share of resources that is available to the community).

2.3.2 Individual home range formation

Besides different submodels of foraging movement included in this part of the model, individual home range formation is implemented as described in Buchmann et al. (2011a). We therefore only provide a short model description here – a complete model description following the ODD protocol (Grimm et al. 2010) is provided in Appendix 2.A. The model was implemented in C++ (source code available upon request from the corresponding author).

We consider a community of mammals consuming and competing for primary production (i.e. herbivores and primarily herbivore omnivores) in which individuals are characterized by their body mass, which is drawn for each animal from a continuous so-called ‘input distribution’ between 0.005 and 100 kg (a reasonable body mass range considering landscape dimensions, compare e.g. Harestad and Bunnell 1979). As an input distribution, we here used a truncated power law distribution with an exponent of -1.5 (a value in the range tested by Buchmann et al. 2011a, yielding realistic community structure).

Animals of different weights are randomly drawn from this distribution. For each animal a search for the most efficient home range in the landscape is performed by testing all suitable/productive grid cells in the landscape in random order as potential central home range cells (‘core’ cells). The grid cells surrounding the potential core are inspected with increasing distance (assuming periodic boundary conditions) by checking what amount of resource could be consumed there and what locomotion costs would have to be spent to reach the respective cell (in case of home range establishment). Here, different foraging movement and search pattern are systemtically compared (see below). The home range search is considered successful if the daily food requirements of the animal can be met by the surrounding area of that core cell without exceeding the extent of the landscape or a maximum home range size. After all cells have been tested as potential core cells, and at least one corresponding home range has provided sufficient resources, the animal settles in the smallest of all potential home ranges identified in this process. Next, the resources are reduced in each home range cell by the consumed amount. Thus, this algorithm assumes optimal foraging of individuals and that home ranges are circular and controlled by distribution of resources and resource competition.

As animals are characterized by their body mass, all parameters can be calculated by empirically determined allometric relationships. The daily food requirements are taken from the allometry of field feeding rate for mammals from Nagy (2001), and locomotion costs per distance from an allometric equation given by Calder (1996). As maximum home range size, we apply a combination of the maxima of constraint spaces for home size of herbivore and omnivore mammals given in Kelt and Van Vuren (2001). To be able to balance locomotion costs and resource gain, locomotion costs are transferred into a resource equivalent by a conversion factor for non-fermenting herbivores (Nagy 2001).

The share of resource production available in a grid cell which is exploitable (for the search) and consumed (in case of home range formation) by an individual is also implemented to vary allometrically with body mass with a scaling exponent of -0.25. Such scaling was previously discussed as explaining the body mass scaling of home range size (e.g. Harestad and Bunnell 1979, Holling 1992, Haskell et al. 2002, Jetz et al. 2004, Buchmann et al. 2011a). The coefficient of this scaling relationship is a model parameter (γ_{PI}, here $\gamma_{PI} = 4 \times 10^{-2}$) (for sensitivity analysis see Appendix 2.B).

2.3.3 Community assembly

Individuals are sequentially drawn from the body mass input distribution, perform a home range search and, if the search is successful, settle down and deplete a part of the resources in the home range. Thus, later individuals face a partly depleted resource landscape. Hence we model a simplified community with only one type of resource which all individuals consume and compete for. Time is not considered explicitly, that is we do not assume a specific time between consecutive 'arrivals' of animals. Moreover, the process of home range search and formation does not include a temporal component. The procedure of drawing the body mass of animals out of the input distribution and performing an optimal home range search for these individuals is stopped when a certain percentage of community resources are distributed among the animals. This percentage is a model parameter (SAT) and determines the degree of community saturation (for implementation and sensitivity analysis see Appendix 2.A ('7.3 Submodel: community saturation') and Appendix 2.B, respectively; for simulation experiments we use SAT = 0.95).

2.3.4 Foraging movements

We here distinguish three different general models of foraging behaviour. These models differ in the costs that an animal pays for integrating a specific resource patch (i.e. grid cell) into its home range. This means that foraging movement is only implicitly modelled via movement costs that correspond to a particular mode of foraging movement. We quantify these costs from an allometric function for the locomotion costs per distance (see above) applied to the (daily average) effective distance the animal needs to move to get resources from a given cell. This distance (DC) differs between the three foraging types.

2.3.4.1 Central place forager (CPF)

Central place foragers (CPF), but also other mammals that live in dens or have nests, at least during certain time periods, for example while raising young, have a strong focus on one central place in their home range which is visited very frequently (Owen-Smith et al. 2010). Because of this high frequency, such behaviour implies a dependence on good habitat quality and high resource availability close to the central place (compare Rhodes et al. 2005). Foraging grounds in the periphery entail high movement costs, as usually food is taken up or collected in these feeding areas and not on the way there or back. An approach for incorporating these principles into a model of optimal home range formation was introduced by Mitchell and Powell (2004). Here, adding a cell to the home range during the search bears locomotion costs on daily average. These costs are calculated for the distance (DC) from the respective cell to the home range core cell, the central place (Fig. 2.2a). For animals it is therefore most efficient to have many resources in close proximity to the central place, allowing for small home ranges which are less costly. This approach was already successfully used in a previous modelling framework to predict community structure, specifically the allometric scaling of home range size and individual abundance (Buchmann et al. 2011a). In analogy to this study, we implemented this approach here only considering suitable grid cells during the home range search, i.e. animals are assumed to not spend energy for a foraging bout to a cell if this cell does not provide any resources. However, unproductive cells increase movement distances to productive cells and thus add to locomotion costs for these latter cells.

2.3.4.2 Patrolling forager (PF)

A contrasting foraging strategy would be an animal which patrols its home range, without frequently returning to the central place, but which is feeding ‘on the way’. Therefore, feeding areas in the periphery of the home range are less costly for such an animal compared to CPF behaviour, since resources can be taken up while moving to this area. Such foraging behaviour is modelled by calculating the ‘cost-effective distance’ DC for each cell as the average distance from neighbouring cells (i.e. 1.207 grid units or 12.07 m, compare Fig. 2.2b). In this foraging movement model, all grid cells (including non-productive) are considered for the home range search (with the non-productive bearing costs without providing resources), because on such a patrolling forage trip, non-productive cells are also assumed to be visited.

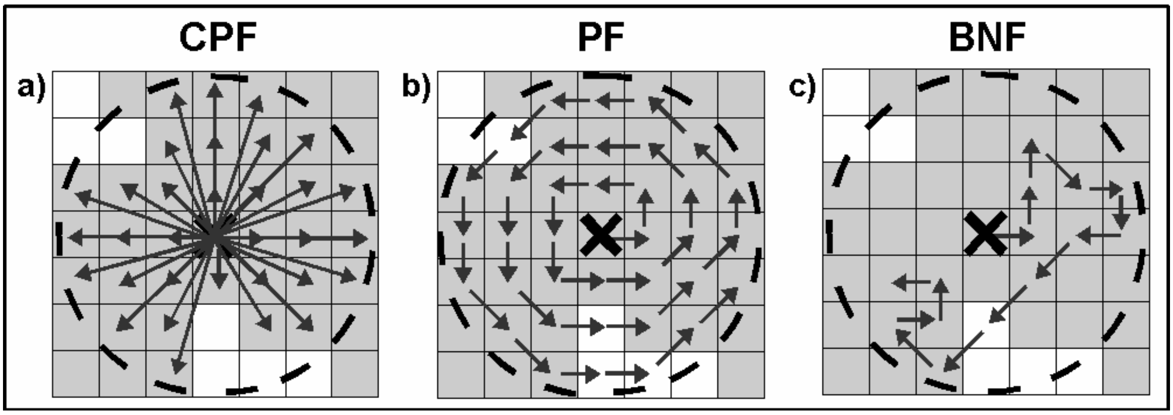

Figure 2.2. Schematic Illustration of foraging and movement principles that are associated with three different foraging movement models. Length of arrows indicate the distance (DC) accounted for locomotion cost for the respective cells. White grid cell symbolize unsuitable habitat. a) In the CPF movement model (sensu Mitchell and Powell 2004), each grid cell in the home range is (on daily average) accounted for locomotion costs for the distance (DC) to the central cell. This represents a strong focus on and high revisiting frequency of the home range centre. Unsuitable habitat is not considered to be the target of foraging bouts. b) Exemplary movement path of a PF animal which patrols its home range on a daily basis but forages 'on the way'; patrolling movements do not exclude unsuitable habitat patches. In c) arrows also illustrate an exemplary movement path of a larger animal following the BNF model. Here, animals also forage on the way (also crossing unsuitable habitat patches), but empirical daily movement distances are considered by scaling DC with a body mass dependent factor. Thus, the model allows larger animals to behave 'nomadically', i.e. only visiting a part of their home range on a daily basis (going along with lower daily average costs per home range cell for larger animals).

2.3.4.3 Body mass dependent nomadic forager (BNF)

Particularly larger animals often show nomadic behaviour within their large home ranges, which means that they are not patrolling their home ranges on a daily basis, but forage in different areas within the home range over time (we use the term 'nomadic' for within home range movement in accordance to e.g. Fielden 1991, Tristiani et al. 2003, Houle et al. 2010, for discussion and references about the use of the term 'nomadic' see Owen-Smith et al. 2010). Such behaviour, as well as the body mass dependence of the tendency to show such behaviour, are reflected by the relationship between body mass and average daily movement distance (DMD). Even if the data sets of two studies (Garland 1983, Carbone et al. 2005) exhibit considerable variance, both found a clear allometric relationship of DMD with an exponent of around 0.25. To account for these findings, we modified the previously described PF foraging movement model by calculating the costs involved in adding a new grid cell (productive or non-productive) to the home range for a distance DC that varies with body mass. This variation shall consider that the sum of distances accounted for movement costs on daily average ($\sum$DC) of all home range cells follows approximately the same relationship with body mass as the one found for DMD of non-carnivores (Garland 1983). To achieve this we calculate DC as

$$\mathrm{DC} = \frac{\text{daily accounted distance}}{\text{number of cells in home range}}\,, \tag{2.1}$$

which translates in our modelling context to

$$\mathrm{DC} = \frac{(875\,\mathrm{m} \times \mathrm{M}^{0.22})}{(1107\,\mathrm{cells} \times \mathrm{M}^{1.05})} = 0.79 \times \mathrm{M}^{-0.83} \text{ (in meter per cell, M in kg)}, \tag{2.2}$$

using Garland's equation for non-carnivores as daily distance that is accounted for locomotion costs. The allometric equation for the number of home range cells is obtained as a combination (the mean of coefficients and exponents) of reported allometric relationships for home range size of mammals (herbivores and omnivores: Harestad and Bunnell 1979, Ottaviani et al. 2006; herbivores: Holling 1992).

The allometric equations for home range size and data on daily movement distance reported in the literature vary considerably (Garland 1983). To examine whether this variability affects our model output, we estimated allometric equations for DMD from 100,000 nonparametric bootstrap re-samples of the DMD data (Garland 1983, non-carnivore data). These equations were then combined with each of the five allometric equations of home range size (see above) to yield 500,000 bootstrap equations for DC (analogous to Eq. 2.2). We then ran model simulations for those bootstrap equations that yield the 5%- and 95%-quantiles of DC for an animal with 1 kg body mass (exponents of -0.70 and -0.873 and coefficients of 0.24 and 4.24, respectively). Yet, this variation in DC allometry had negligible effects on model outputs (results shown in Appendix 2.B).

2.3.5 Analysis of simulation results

To describe community-level effects of simulated habitat loss, we use the individual size distribution (ISD) of the resulting model community (see Appendix 2.C for sample distributions). It has been shown earlier (Buchmann et al. 2011a) that the ISD can be well described by a power law distribution. The exponent of this body mass distribution is determined by a maximum likelihood fit. Moreover, the 95%- quantile of body mass, the maximum body mass as well as the number of individuals of each simulation community is compared for the different foraging models.

2.4 Results

In a first step we tested the three foraging models for a single individual in a homogenous resource landscape in order to better understand the efficiency of the different foraging strategies for different body masses (Fig. 2.3). 'Efficiency' here means the cumulative net energy gain, i.e. the balance of energy gain and related costs in increasing home range size. In general animals first gain energy when adding grid cells to the home range during the search. For small animals (0.01 kg) CPF behaviour (each home range cell 'costs' the distance DC to the home range core) is as efficient as the PF (each cell 'costs' the distance DC to any neighbouring cell) and the BNF model (the sum of DC is oriented towards body mass dependent daily movement distances). For animals with a body mass of 1 kg, the PF and the BNF model still provide the same amount of resources, while the CPF approach starts to be less efficient. For animals of 10 and 20 kg, the BNF model allows the highest resource gain, while CPF is not useful for obtaining resource benefits from the ~ 250th and the ~ 40th cell, respectively.

Testing, in a second step, community-level responses in fragmented landscapes reveals that changes in both the community saturation level (SAT) and variation of the resource share an individual can exploit in a grid cell (γ_{PI}) impact the resulting communities similarly for all three foraging movement models. Furthermore, comparing the three foraging movement approaches with regard to home range scaling and the exponent of the community ISD (power law distribution) for moderate fragmentation and habitat area shows that results of all approaches agree well with empirical data (see Appendix 2.B). For further comparisons of empirical patterns and model predictions see Buchmann et al. (2011a).

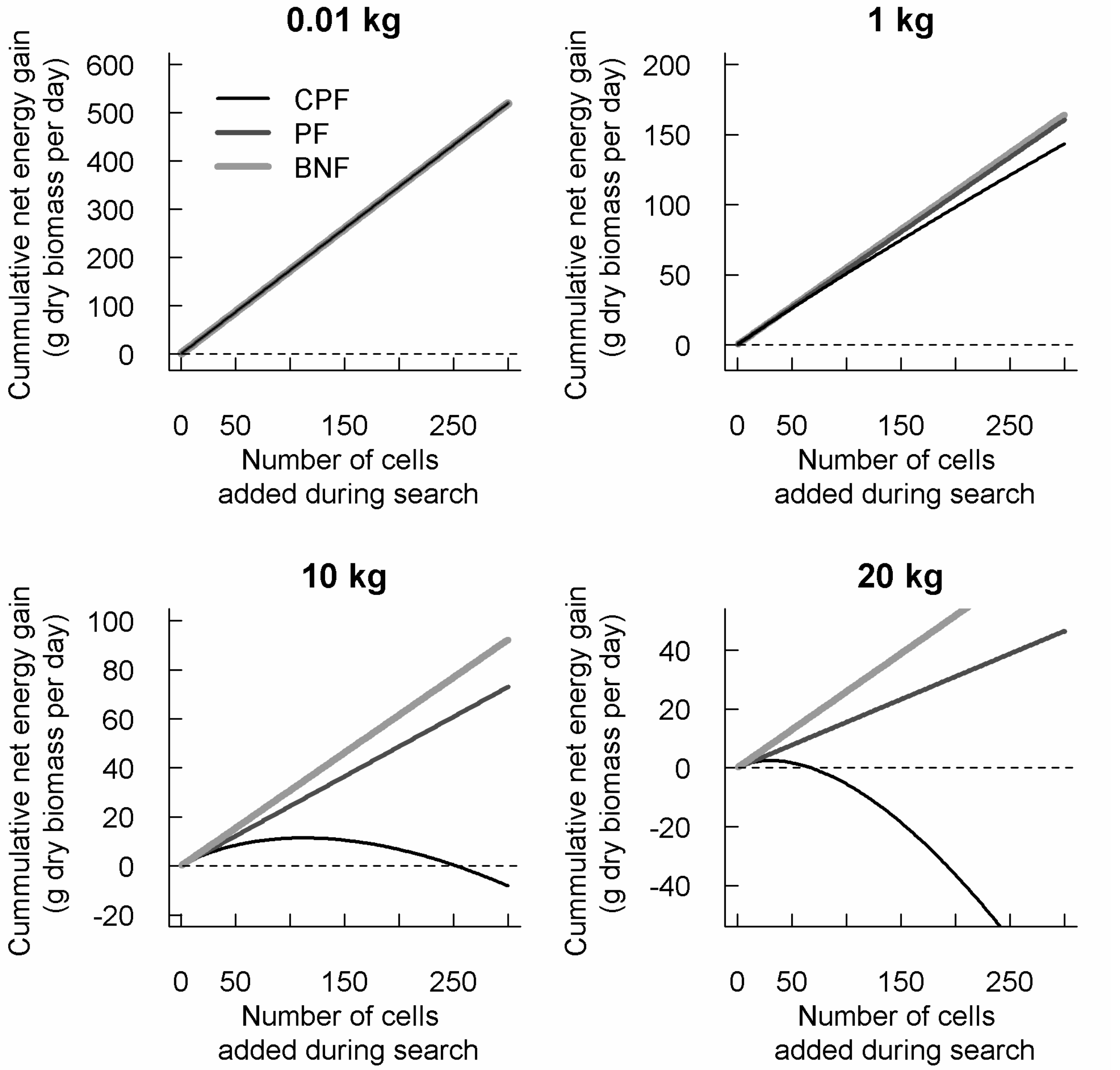

Figure 2.3. Cumulative net energy gain for the first 300 grid cells added during home range search for the three foraging movement approaches and different animal body masses. Results shown are model predictions for a single animal that is randomly located into a homogeneous resource landscape (suitable area of 100%, all cells with average resource production).

As expected, the composition of model communities changes with loss of suitable habitat and in dependence of the foraging movement model applied (Fig. 2.4). The ISDs of mammal communities are generally less steep for BNF movement than for PF, which again yields less steep ISDs than CPF behaviour. Interestingly, for PF and BNF foraging movement models, the exponent of the body mass distribution shows a relatively stable level until a certain threshold of habitat loss is reached. With further loss of habitat, the community composition shifts strongly to relatively less large animals (Fig. 2.4). These thresholds can be recognized at ~ 40-50% suitable area. In contrast, the response of the ISD to loss of habitat area is much weaker for CPF movement. The scaling exponent of the body mass distribution is only slightly affected (shifted to more negative values) with less habitat area.

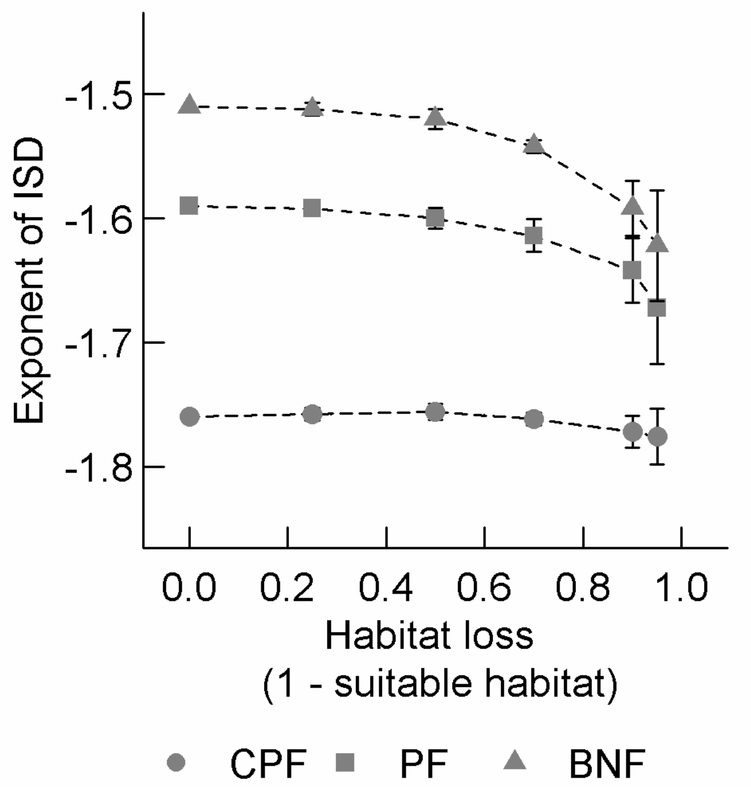

Figure 2.4. Exponent of the ISD of model communities, with three different foraging movement models (see legend). Grey symbols give means of five landscape replicates, error bars 95% C.I.s.

A clear distinction between the three foraging movement models also can be seen when the 95%-quantile and maximum of the body mass distribution of the resulting communities are compared. Both measures show a clear response to habitat loss for all foraging types (Fig. 2.5a-c and d-e). Communities simulated with BNF movement show a strong increase of the maximum and 95%-quantile of body mass with increasing habitat area (and hence also available resources in the landscape, Fig. 2.5c and f) compared to PF, which again is more sensitive to habitat loss than the CPF strategy. Similar to the exponent of the ISD, the 95%-quantile of body mass saturates at higher levels of suitable habitat, i.e. no larger animals can establish home ranges even if more habitat and hence resources are available. This saturation is occurring for high amounts of remaining habitat (little habitat loss) with BNF movement. In contrast, using CPF strategy, the 95%-quantile of body mass (as well as the maximum) are not further increased already at low levels of habitat area (high habitat loss).

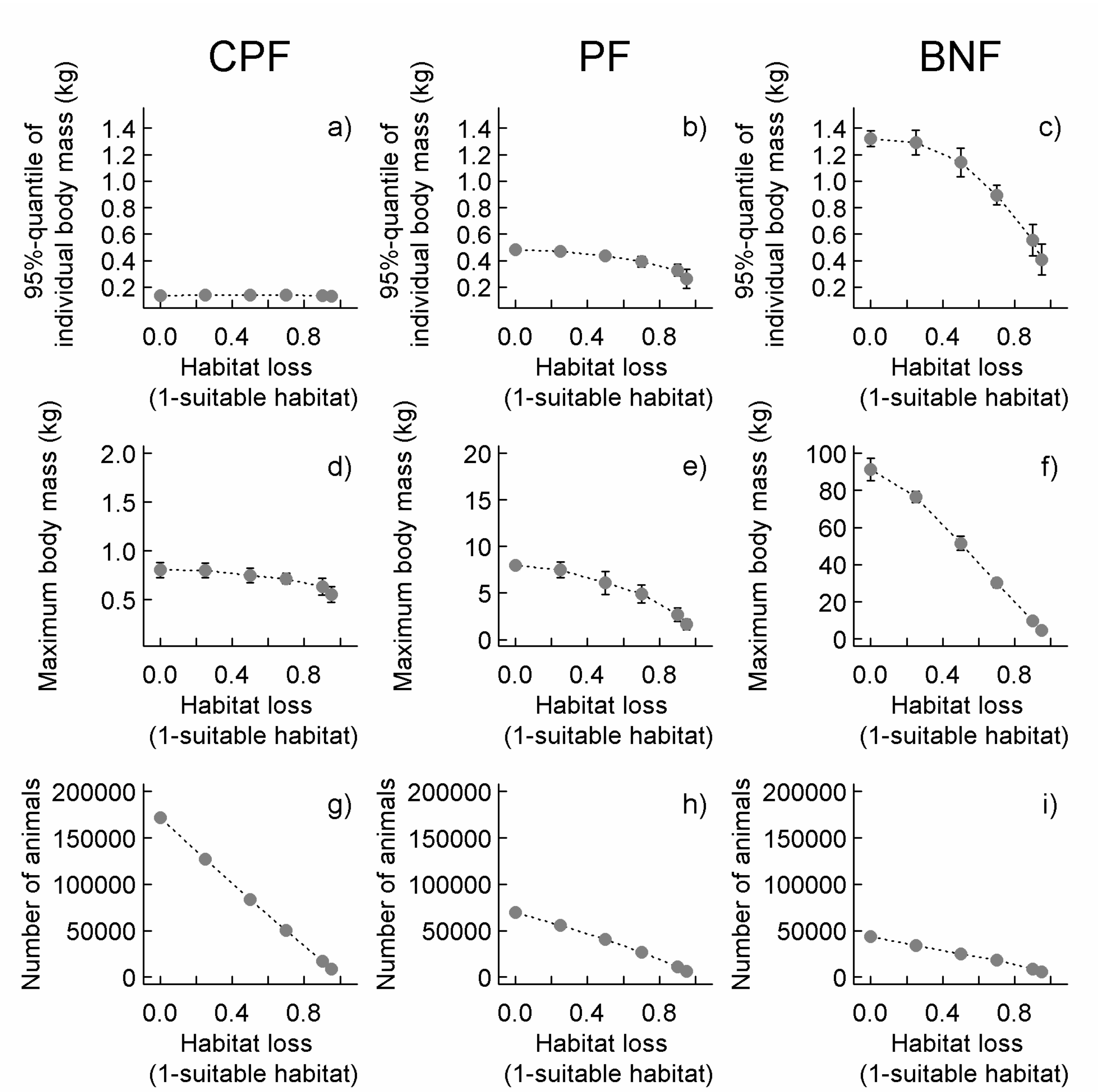

Figure 2.5. 95%-quantiles of body mass (a-c), maximum body mass (d-f, note different scaling of the y-axes), and number of animals of model communities (g-i) for three different foraging movement models (on the left side central place foragers, in the middle patrolling foragers and on the right side body mass dependent nomadic foragers). Circles give the means of five landscape replicates, error bars 95% C.I.s.

As expected, the number of individuals in the resulting communities of all foraging types increases with the proportion of suitable habitat (and thus resources) in the landscape (Fig. 2.5g-i). However, foraging movement models clearly differ in that resulting communities of CPF animals have more individuals and react stronger to habitat loss, whereas BNF movement allows the least animals to establish a home range and is less sensitive to habitat loss than the other two approaches. PF behaviour shows an intermediate response to habitat loss.

2.5 Discussion

This modelling study is, to our knowledge, the first that investigates the effect of habitat loss on the individual size distribution (ISD) of a terrestrial mammal community. Moreover, the presented modelling concept allows for testing the effects of individual foraging movement (Fig. 2.2) on community structure (namely the ISD) and on the corresponding reaction of communities to habitat loss (Fig. 2.1). Generally, ISDs of terrestrial communities are not well studied and mechanistic understanding of these complex patterns is still poor. This is mainly due to the fact that appropriate data is very difficult to obtain (Buchmann et al. 2011a). Since most studies which investigate the effects of habitat loss and fragmentation look at either species richness of communities or only at the abundance of single species (Debinski and Holt 2000) it is not possible to directly compare our findings to empirical observations. Following a pattern-oriented approach (sensu Grimm et al. 2005 and May et al. 2009) this lack of data currently only allows to compare more general patterns such as the allometry of home range size (see Appendix 2.B), the existence of extinction thresholds with increasing habitat loss or the general pattern of increased sensitivity of larger animals to habitat loss (see also Buchmann et al. 2011a for comparisons of the CPF model output with empirical data). This lack of data in terrestrial systems stands in stark contrast to aquatic studies, where community body mass or biomass distributions are more often available, for example through fisheries assessments (White et al. 2007).

A simplified model scenario with homogeneous resource distribution (Fig. 2.3) reveals that the efficiency of different foraging strategies varies as a function of animal body mass. While for small animals (< 1 kg) a CPF movement strategy is still efficient, for larger animals (> 1 kg) this foraging mode starts to be less and less efficient. The larger the animal is, nomadic behaviour without a specific focal point in the home range (the BFN movement model) becomes more efficient, compared to CPF, but also to the PF foraging strategy. Figure 2.2 illustrates the enormous accumulation of movement costs associated with the CPF type the larger the home range gets (which is the case for larger individuals). This is due to the fact that distances to closer cells have to be 'paid' again when moving to more distant cells, since no foraging on the way is allowed (compare also Buchmann et al. 2011a). Hence, large animals are limited by high foraging movement costs associated with the centre-focused movement pattern, and even a higher share of suitable habitat does not enable larger animals to establish larger home ranges in the community. However, more habitat area and overall resources strongly increase the overall number of animals, since the community consists mainly of small individuals that have low resource requirements. Interestingly, within this community the ratio (in terms of abundance) of small and larger individuals remains unchanged, reflected in the constant exponent of the ISD of CPF scenarios.

The relationship between body mass and foraging movement strategy may also explain mass-specific differences in the reproductive strategies of mammals. The fact that raising altricial young requires a very centre-focused foraging movement pattern may explain why many small mammalian herbivores (e.g. most rodents) are altricial, whereas most larger herbivores (e.g. ungulates) raise precocial offspring.

Even if individuals with different body masses perform differently, dependent on foraging strategy, all three foraging movement approaches agree in predicting a shift towards fewer large and relatively more small individuals in the community with increasing habitat loss. This is reflected in a decreasing exponent of the ISD (Fig. 2.4) and in a reduced mass of the largest animals in the community. The total number of individuals in the community is decreasing with less suitable habitat and thus less available resources (Fig. 2.5). These results correspond well with empirical findings: Ewers and Didham (2006) showed that large animals are expected to be more vulnerable to habitat loss. One major reason for their proneness to extinction is their low population density. Both effects, i.e. the higher vulnerability of large animals to habitat loss and their low abundance, are reflected in our simulation results, and hence they can to some degree be mechanistically explained by individual space use characteristics, considering physiology, optimal foraging principles and locomotion costs involved in different foraging strategies. However, also other types of movement such as dispersal (natal or breeding dispersal) can be essential for the maintenance of populations (Nathan et al. 2008). These movement types are also influenced by different behavioral and physiological processes that can be strongly influenced by landscape structure (e.g. individuals that move within territories have a previous knowledge of the landscape while dispersing individuals do not). Moreover, factors, such as social interactions or lifespan which can affect community responses to habitat modifications (e.g. Ewers and Didham 2006, Banks et al. 2007) are not included in our parsimonious modelling framework.

Besides a generally greater share of larger individuals, communities of non-centre-focused animals (with both the PF and the BNF models) show a stronger decrease of the 95%-quantile and the maximum of body mass as well as of the exponent of the ISD with habitat loss compared to CPF communities. These foraging movement models allow 'foraging on the way' during movement. Therefore, they assume lower movement costs in larger home ranges and do not cause a sharp movement-induced limit like communities of centre-focused animals. Generally, communities with body mass dependent movement (BNF), allowing for efficient nomadic foraging of large animals, have a higher number of larger individuals, and, since these individuals consume a great amount of resources, they also have fewer individuals in total than the communities with PF animals. Nomadic foraging is expected to be particularly efficient when resources are patchily distributed (Mueller and Fagan 2008). This corresponds well to our finding that large animals of BNF communities can initially compensate for increasing habitat loss in fragmented landscapes as indicated by the limited response of the 95% body mass quantile up to a critical threshold of habitat loss. Larger BNF animals seem to be abundant up to moderate levels of habitat loss because they can still make use of scattered resource patches in their large home ranges. Beyond a certain level of habitat loss, however, this compensation is not possible anymore, and the resources are divided up between smaller individuals, leading to an accelerated response of the body mass distribution (exponent, 95%-quantile). Interestingly, up to this critical level of habitat loss, the exponent of the ISD responds more slowly than the 95%-quantile (and also the maximum) of this distribution, especially for the BNF movement type. This suggests that, when the largest herbivores in the community disappear, the next smaller size class benefits most. With regard to the ISD exponent, the corresponding increase of medium sized herbivores partly compensates for the loss of larger individuals. This resembles the phenomenon of mesopredator release known from carnivore communities (Crooks and Soulé 1999): as large species disappear, medium sized species can increase in abundance filling in the available niche space. To our knowledge, similar phenomena have not yet been reported for herbivores, and their existence thus remains to be tested for in empirical studies. However, given the inevitable limitations of the generic modelling approach used here, future model extentions should examine the role of alternative, only partly overlapping resource types for differently sized herbivores and the assembly of mixed communities that comprise all three foraging modes.

Different studies report critical levels of habitat area, a so called ‘extinction threshold’ below which there is an accelerated extinction probability for many species (Harrison and Bruna 1999, Fahrig 2002, 2003, Ficetola and Danoël 2009). A classical way of explaining such a threshold response to landscape change is the ‘percolation theory’ (With and Crist 1995), which predicts sudden changes in species performance when connectivity between patches falls below critical values that inhibit species dispersal. The results of our simulation model, especially for the PF and BNF strategies, suggest that individual space use characteristics in face of competition can be an alternative explanation for observed extinction thresholds.

2.6 Conclusion

Although it is known that i) the spatial distribution of resources affects the foraging ecology of species and hence movement pattern within a home range (Ottaviani et al. 2006), and that ii) movement affects population performance (Morales et al. 2010), there is currently no study that relates foraging behaviour to community changes under habitat loss. Clearly our three foraging movement models and the community model itself are strong simplifications of real systems. More refined movement models with explicit individual movement paths (see Börger et al. 2009, Van Moorter et al. 2009) could be integrated into the framework used here. These could also consider additional costs in fragmented landscapes such as costs related to an increase of predation risk or increased physiological costs in unsuitable matrix patches. However, it is questionable whether such more complex models could readily be applied to entire communities.

Our model helps to understand basic principles of how foraging strategy affects community structure in face of habitat loss and thus constitutes a good basis for further studies. This could include the implementation of the modelling framework for specific species (compare Buchmann et al. 2011a) with different foraging strategies. New advancements in telemetry and satellite tracking methods (Cagnacci et al. 2010) are promising and may soon deliver the necessary movement and abundance data at the community scale. In combination with advanced remote sensing techniques (Mueller et al. 2008) providing high resolution data on resource distributions such information would help to test and validate our findings and, as a next step, could be used to apply similar modelling concepts for specific questions on the conservation and management of communities.

2.7 Appendix 2.A – Model description following the standard ODD – protocol

1 Purpose

The purpose of our model is to simulate community assembly in order to explain and investigate the structure, specifically the individual size distribution (ISD, after White et al. 2007) of herbivorous mammal communities. This is done on the basis of individual physiology and space use characteristics, including the cumulative effects of foraging movement and resource competition between individuals. The model furthermore allows for the investigation of landscape effects (e.g. habitat loss) on community structure in dependence of these mechanisms.

2 Entities, state variables and scales

The model is spatially explicit and is based on grid-based simulation landscapes. These landscapes, consisting of 257 × 257 grid cells, each interpreted as 10 × 10 m, represent the distribution of daily resource production (grid cell values). With increasing model run time (which can be interpreted as assembly history), this available daily resource production in landscape grid cells decreases as more and more mammals incorporate grid cells in their home ranges and consume part of the resources produced (this amount consumed is also calculated as daily consumption).

The model simulates resource dependent home range formation of individual mammals. These are characterized by their body mass (ranging between 0.005 and 100 kg) and as mammals consuming plant diet (i.e. herbivores and primarily herbivorous omnivores). Moreover, individuals are characterized to be of one of three possible foraging movement types (central place forager CPF, patrolling forager PF, or body mass nomadic forager BNF). Because all individuals have a specific body mass, well established allometric relationships can be used to calculate individual daily resource requirements and specific locomotion cost (per distance moved). Maximum home range size and the share of biomass that an individual can access from the biomass available in each grid cell (both on a daily basis) are also implemented to vary allometrically with body mass (for details see ‘7.1 Submodel: Individual home range search’).

3 Process overview and scheduling

Community assembly is modelled on the basis of three major steps:

1. A mammal is assigned a specific body mass, drawn from a continuous, so-called ‘input distribution’.
2. For this mammal all suitable grid cells in the landscape are tested as potential central home range cells. This is done by adding grid cells with increasing distance to the potential home range until the food requirements of the animal can be satisfied on basis of the respective area or until an empirically determined (allometric) maximum home range size is exceeded. For each cell that is added to the potential home range during this search process, resource gain from the cell and movement costs (both body mass dependent) associated with inclusion of this cell into the home range are balanced (for detailed description of this model compartment, see below: ‘7.1 Submodel: Individual home range search’). Different types of foraging movement can be incorporated into the modelling framework by a different calculation of movement costs for each home range cell (see below: ‘7.2 Submodel: Foraging Movements’)
3 After all suitable grid cells have been tested as potential central cells, and at least one home range search was successful (i.e. the area necessary to cover the mammal’s resource requirements does not exceed the maximum home range size), the animal settles in the smallest of the possible home ranges and the resources within this home range are depleted (by a body mass dependent amount, see above: ‘2 Entities, state variables and scales’, and below: ‘7.1 Submodel: Individual home range search’).

These steps are repeated until a certain level of system saturation (SAT) is reached. This saturation is determined via the amount of available resources that is consumed by the simulated community (for details see below: ‘7.3 Submodel: Community saturation’). Thus, the scheduling of the model is event driven (the ‘arrival’ of individuals and establishment of their home ranges as events), and the time between these events is not explicitly defined. The process of home range search and establishment itself does not have a temporal component either.

4 Design concepts

4.1 Basic principles

A basic concept of the model of individual home range formation in mammal communities are the characterization of individuals by their body mass only, which allows the application of allometric relationships in order to calculate resource needs, specific locomotion costs per distance moved, individual resource availability and maximum home range size.

The search of an individual home range is based on an area minimizing principle adopted from optimal foraging theory (Mitchell and Powell 2004). The establishment of individual home ranges is controlled by the spatial distribution of available resources as well as by individual physiology and foraging behaviour. The effect of foraging movement type on community structure is systematically tested (see '7.2 Submodel: Foraging movements'). Resource consumption within the home range changes the spatial resource distribution in the landscape and hence implies competition between individual mammals. Community assembly is simulated on the basis of resource production and reduction, individual allometric resource requirements and consumption, as well as foraging movement type (with the respective movement distances), all calculated and balanced on a daily basis.

4.2 Emergence

Major model output is the presence of individual mammals of certain body sizes in the community, that is the distribution of individual body masses (or the individual size distribution, ISD). In this emerging community all individuals inhabit a home range with a specific location and size. Based on the model algorithms the abundance of individuals of a certain size depends on landscape properties and foraging movement. The same is the case for their home range sizes and locations, which of course additionally depend on the body mass (home range size an location are, however, not in the focus of this study; for more detail regarding this aspect see Buchmann et al. 2011a).

4.3 Adaptation

Individual mammals adapt the size of their home range to current resource conditions. If resources are sparse ore less spatially concentrated, home ranges have to be larger to fulfil the 'inhabitant's' resource requirements (home range size is, however, not in the focus of this study; for more detail see Buchmann et al. 2011a).

4.4 Objectives

The major objective of individual mammals is to minimize the area of their home range. Technically this is achieved by choosing that location in the landscape to 'settle down' which allows for the smallest possible home range.

4.5 Interaction

All individuals in the community interact by consuming and hence competing for the same (type of) resource in the same landscape.

4.6 Stochasticity

Stochastic components in the model are the generated landscapes on the one hand and the (sequence of) body masses drawn from the input distributions. The variability caused by these stochastic model elements is considered by simulating 5 (landscape) replicates for each scenario.

5 Initialization

The model reads in simulation landscapes that are characterized by the spatial autocorrelation of grid cell values (daily resource production) which determines the level of fragmentation of suitable (productive) habitat (Saupe 1988, Hargrove et al. 2002, Körner and Jeltsch 2008). For all simulations we use moderate spatial autocorrelation (Hurst-factor H = 0.5, $\sigma^2 = 30$), i.e. fragmentation remains unchanged. For different habitat loss scenarios, however, landscapes with different area of suitable habitat are used. The (non-0) grid cell values of all landscapes used in simulations follow the same normal distribution (with an average productivity of 6.85×10^{-2} kg dry biomass × grid $\text{cell}^{-1} \times \text{day}^{-1}$, oriented towards the productivity of typical shrub lands and grasslands, Whittaker 1975). We generally assume that 20% of this productivity is available to the mammal community (the remainder is assumed to either not be consumable or to be lost to other taxonomic groups, see Buchmann et al. 2011a for analyses of the effects of landscape fragmentation and the share of resources that is available to the community).

Initially, all simulation landscapes are rich in available resources, and do not yet ‘harbour’ any mammals. In the course of the simulation, and successful home range establishments, the community grows and available resources in the landscape get reduced. As input distribution (out of which individual body masses are drawn), we use for all scenarios a truncated power law distribution of the form

$$p(M) = \kappa \times M^{\eta}, \qquad (2.A.1)$$

with p representing the probability density of a certain body mass M. The normalization constant κ is chosen so that equation 2.A.1 integrates to 1. As exponent η we use -1.5 for all simulations (a value in the range tested by Buchmann et al. 2011a, yielding realistic community structure).

The two major model parameters for all simulation experiments to explore the effects of habitat loss and foraging movement on community structure are set as follows: γ_{PI}, determining the general magnitude of resource use of individuals (for details see ‘7.1 Submodel: Individual home range search’) is set to 0.04; SAT, determining community saturation (see ‘7.3 Submodel: Community saturation’) is set to 0.95 (for sensitivity analysis of both parameters see Appendix 2.B).

Finally, communities consisting of animals of either of three fundamentally different foraging movement types are simulated for different levels of suitable habitat. These are: central place forager (CPF), patrolling forager (PF) and body mass dependent nomadic forager (BNF) (for details see ‘7.2 Submodel: Foraging movements’).

6 Input data

The model does not use input data to represent time-varying processes, as time is not modelled explicitly.

7 Submodels

7.1 Submodel: Individual home range search

This submodel does not simulate explicit daily behaviour of individuals, but the cumulative effects of resource use and competition in space in combination with foraging behaviour (with corresponding movement costs).

For each individual, all suitable grid cells are tested for their potential to serve as the centre of a circular home range. Assuming periodic boundary conditions grid cells are added to the home range with increasing distance to the possible core cell. Cells are added and the mammal can gain energy from these cells until the daily energy requirement of the animal is fulfilled. The latter is calculated as the daily field feeding rate FR. After Nagy (2001) this rate scales for all mammals as

$$\mathrm{FR} = 0.055 \times \mathrm{M}^{0.74} \quad \text{(kg dry biomass} \times \text{day}^{-1}\text{, M in kg).} \qquad (2.A.2)$$

Daily energy gain of an individual $\mathrm{IG_i}$ in each cell i is calculated as the part of the daily productivity in each grid cell which is available to the community $\mathrm{R_i}$ (note that generally only 20% of the biomass that is produced daily is available to the community for consumption, see ‘5 Initialization’) multiplied by a factor PI. This factor accounts for the part of the available resources in a cell that is exploited on daily average by the individual in case of home range establishment.

$$\mathrm{IG_i} = \mathrm{R_i} \times \mathrm{PI} \quad \text{(kg dry biomass).} \qquad (2.A.3)$$

The factor PI for individual resource use is implemented to vary with body mass:

$$\mathrm{PI} = \gamma_{\mathrm{PI}} \times \frac{\mathrm{M}^{-0.25}}{0.001\mathrm{kg}^{-0.25}} \quad \text{(M in kg),} \qquad (2.A.4)$$

where the coefficient γ_{PI}, determining the general magnitude of PI, is a systematically tested model parameter. The denominator (0.001 $\mathrm{kg}^{-0.25}$) was chosen to ensure that PI varies between 0 and 1. Such allometric variation of individual resource availability is discussed in the context of the allometry of home range size (e.g. Holling et al. 1992, Haskell et al. 2002, Buchmann et al. 2011a).

The net energy gain of individuals IGN_i in each cell i is calculated as

$$IGN_i = IG_i - LC_i \qquad \text{(kg dry biomass)}, \qquad (2.A.5)$$

where LC_i, are the locomotion costs of travelling to cell i. Allometric relations for movement costs per unit distance MC are taken from Calder (1996):

$$MC = 10.70 \times M^{0.68} \qquad (J \times m^{-1}, \text{M in kg}). \qquad (2.A.6)$$

We convert MC into the locomotion cost LC_i of reaching grid cell i, using

$$LC_i = \frac{DC_i \times MC}{f} \qquad \text{(kg dry biomass)}, \qquad (2.A.7)$$

where DC_i is the average movement distance that has to be travelled on daily average to access resources from this home range cell i (for simplicity and better readability in the paper we only use 'DC' for this measure there). As conversion factor f, to express movement costs as equivalent amount of dry biomass, we use 1.00×10^7 J × kg dry biomass intake^{-1}, given in Nagy (2001) for non-fermenting herbivores. The method of determining DC_i, the average daily movement distance for each home range cell, distinguishes three fundamentally different foraging movement types (see next section '7.2 Submodel: Foraging movements').

Cells are sequentially added to the potential home range with increasing distance to the core cell until the animal is satiated ($\sum IGN \geq FR$), or until the required area exceeds a maximum home range size. We calculate this upper limit for each body mass as the maximum of the two equations

$$HR_{max-herb} = 56.23 \times M^{0.91} \qquad \text{(ha, M in kg), and} \qquad (2.A.8)$$

$$HR_{max-omn} = 47.86 \times M^{1.18} \qquad \text{(ha, M in kg)}, \qquad (2.A.9)$$

given in Kelt and Van Vuren (2001) as the maximum of a constraint space of home range area for herbivores (Eq. 2.A.8) and omnivores (Eq. 2.A.9) (both groups can be assumed to consume the primary production in the model).

If a potential home range fulfils an animal's resource requirements within this limit, the algorithm records the area and location of this potential home range. Once all suitable cells have been tested as home range centre, the animal settles in the smallest possible home range. This settling means that resources are depleted by IG_i in each gird cell within the home range.

7.2 Submodel: Foraging movements

We distinguish three different general models of foraging behaviour. They differ with respect to the distance (DC_i) which is accounted for movement costs (see Eq. 2.A.6 and 2.A.7) for integrating any resource patch (landscape grid cell i) into the home range.

7.2.1 Central place forager (CPF)

For this movement approach DC_i (the 'cost-effective distance' of each home range cell) is calculated as the distance from the respective home range cell (which is added to the home range) to the home range centre. Such implementation can be regarded to represent well central place foragers (CPF), but also other mammals that live in dens or have nests, at least during certain time periods, for example while raising young, and which therefore have a strong focus on one central place in their home range which is visited very frequently (Owen-Smith et al. 2010). This approach was initially proposed by Mitchell and Powell (2004) and was already successfully used in a previous modelling framework to predict community structure, specifically the allometric scaling of home range size and individual abundance (Buchmann et al. 2011a). In analogy to this study, the approach is here implemented only considering suitable grid cells during the home range search, i.e. animals are assumed to not spend energy to go to a cell if this cell does not provide any resources.

7.2.2 Patrolling forager (PF)

A contrasting alternative foraging movement strategy is implemented by calculating the 'cost-effective distance' DC_i for each home range cell as the average distance from neighbouring cells (i.e. 1.207 grid units or 12.07 m). This approach reflects animals that are patrolling their home range, without frequently returning to the central place, but which are feeding 'on the way'. In this movement model of a patrolling forager (PF), all grid cells (including non-productive) are considered for the home range search (the non-productive bear costs without providing resources), because on such a patrolling forage trip, non-productive cells are also assumed to be visited.

7.2.3 Body mass dependent nomadic forager (BNF)

This BNF foraging movement approach considers the body mass dependence of daily movement distance (DMD). Therefore, the sum of the 'cost-effective distances' of all home range cells ($\sum DC_i$), i.e. the total distance that is accounted for locomotion costs on daily average for any individual, shall follow the same relationship with body mass as the one found for DMD of non-carnivores (Garland 1983). This is achieved by modifying the PF approach by calculating DC_i as

$$DC_i = \frac{\text{daily accounted distance}}{\text{number of cells i in home range}} \, . \qquad (2.A.10)$$

As enumerator of this equation, we use Garland's (1983) allometric equation. The denominator we calculate by combining reported allometric relationships for home range size of mammals (the mean of coefficients and exponents; herbivores and omnivores: Harestad and Bunnell 1979, Ottaviani et al. 2006; herbivores: Holling 1992).

Thus, in our modelling context equation 2.A.10 translates to

$$DC_i = \frac{(875\,\mathrm{m} \times M^{0.22})}{(1107\,\mathrm{cells\,i} \times M^{1.05})} = 0.79 \times M^{-0.83}$$

(in meter per cell, M in kg). (2.A.11)

7.3 Submodel: Community saturation

Individual mammals get assigned a body mass drawn from the input distribution and a home range search is performed. In case of home range establishment of individuals the community grows and resources in the landscape get more and more reduced. The amount of resources consumed by the community shows a saturation response with model runtime (comparable to the saturation response of the number of animals in the community shown by Buchmann et al. 2011a, however, saturating even more quickly). Simulations were executed (i.e. animals were drawn from the input distribution and for each, a home range search was performed) until 5,000 consecutive individuals were unable to establish a home range (because the resources in the landscape were already too low). This value could be safely assumed to represent 100% saturation, since no more change of the amount of consumed resources could be recognized, already at lower values than 5,000. The respective amount of consumed resources was thus used (as 100%) to calculate the resource level corresponding to the community saturation aimed for in simulation scenarios (e.g. 95%), which was then used as termination criterion for these simulations.

2.8 Appendix 2.B – Model validation and sensitivity analysis

Figure 2.B.1 shows that model predictions for the vast majority of scenarios agree well with empirical data, independently of the foraging movement model applied. For simulations investigating the effect of habitat loss on community structure, we used values of the two major model parameters (γ_{PI} = 0.04 and SAT = 0.95) that lead to good agreement between model predictions and independent data (allometry of home range size: Harestad and Bunnell 1979, Ottaviani et al. 2006, Holling 1992, exponent of ISD: Burbidge and McKenzie 1989, Brown and Nicoletto 1991, for derivation of values see Buchmann et al. 2011a). Model responses to variation in these two parameters are discussed in detail in Buchmann et al. 2011a. Variation in DC allometry (to account for considerable variability in the data of daily movement distance and home range size, see Methods) has a negligible effect on model predictions (Fig. 2.B.1).

The caveat for the BFN movement model is that allometric scaling of home range size is needed as an input to calculate DC. Technically, the model may therefore not be used to predict allometric relationships of home range size. Results of home range scaling produced by this model and the sensitivity of these results to model parameters were, however, not markedly different from the results of the PF movement model. The fact that BNF and PF movement models only differ with respect to a body mass dependent factor for DC indicates that the body mass dependent implementation of DC only affects body mass composition of the community and its reaction to habitat loss, but not the home ranges of individuals.

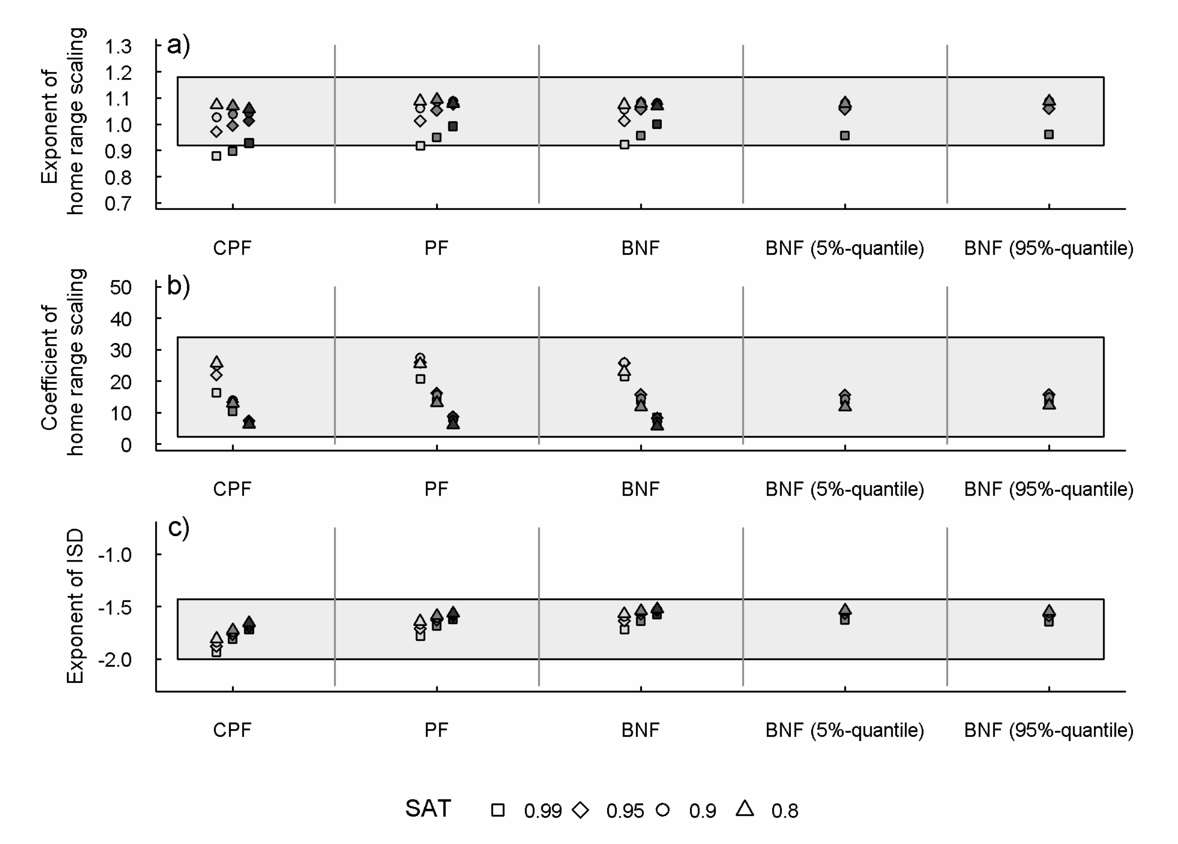

Figure 2.B.1. Validation and sensitivity analysis of the allometric community model of individual home range formation with three different foraging strategies (central place forager CPF, patrolling forager PF and body mass dependent nomadic forager BNF) and of variation of the allometric equation of DC (the locomotion cost-effective distance for each home range grid cell, see Methods) for the BNF model (S = 0.15, H = 0.5, in analogy to Buchmann et al. 2011a). Model results are shown for three major output variables characterizing the allometry of home range size (a-b) and the exponent of the individual size distribution ISD (c) of the community, predicted by the model. Symbols characterize different community saturation SAT (legend) and grey scale values stand for the coefficient of the allometric equation of individual resource availability γ_{PI} (light grey 0.02, medium grey 0.04, and dark grey 0.08, for the effect of variation of DC calculation only γ_{PI} of 0.04 was tested). Grey boxes show the range of comparable empirical data for mammals (allometry of home range size: Harestad and Bunnell 1979, Ottaviani et al. 2004, Holling 1992, exponent of ISD: Burbidge and McKenzie 1989, Brown and Nicoletto 1991, for derivation of values see Buchmann et al. 2011a).

2.9 Appendix 2.C – Exemplary individual size distributions (ISD) of simulated communities

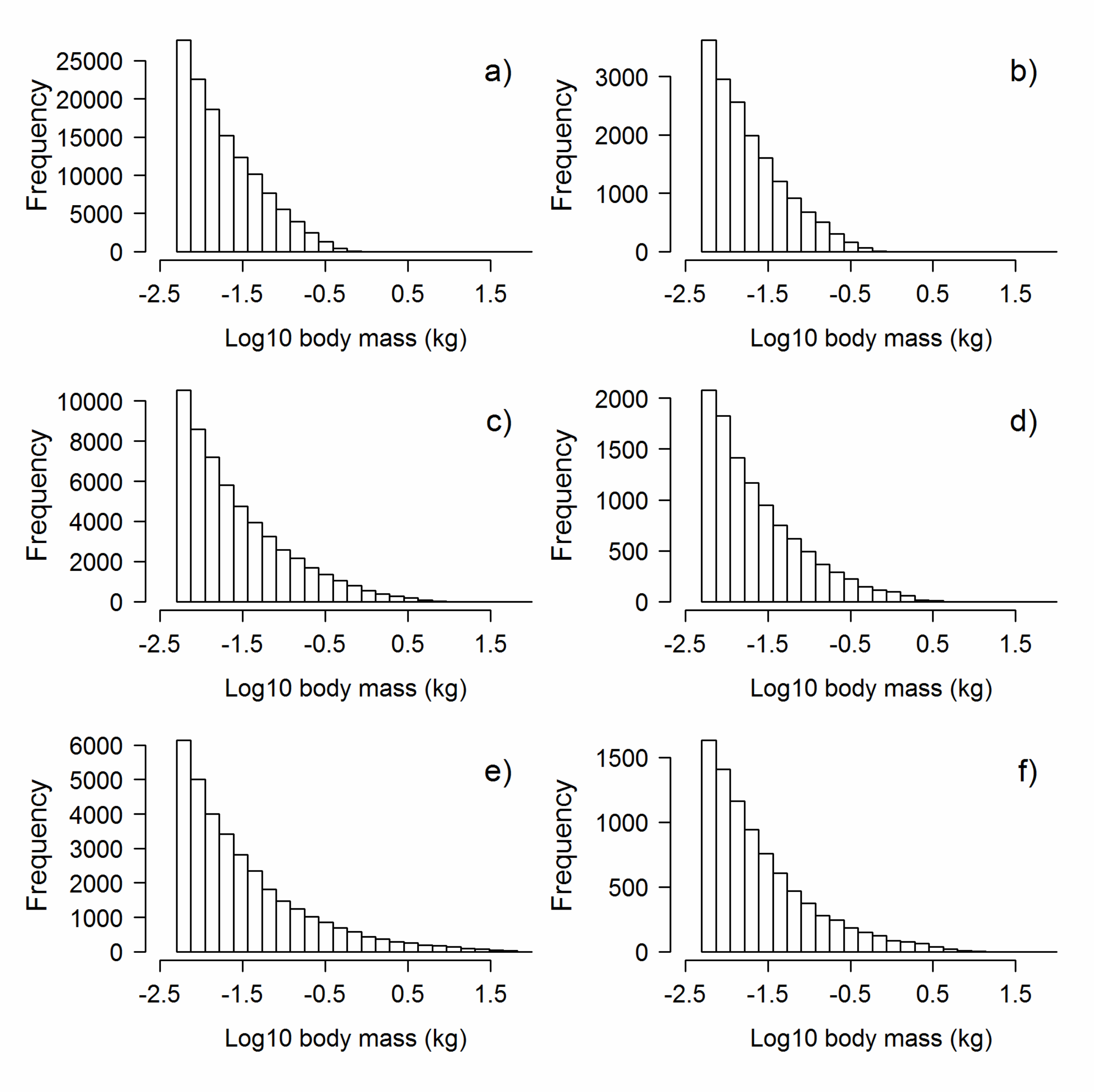

Figure 2.C.1. Sample individual size distributions (ISD) of simulated communities: left column: suitable area 75%, right column: suitable area 10%; a) and b) central place forager CPF, c) and d) patrolling forager PF, e) and f) body mass dependent nomadic forager BNF.

Link to the next chapter

After the allometric model of individual home range formation in terrestrial communities had been introduced and model behaviour had been elaborated and discussed in detail (Chapter 1) the approach was successfully applied to investigate for the first time the role of different foraging movement strategies for community structure and the effects of habitat loss on communities (Chapter 2). Besides the fact that the model is mechanistic and therefore allows the evaluation the importance of different mechanisms, it still is simplistic which opens the possibility of parameterizing it for different taxa. Moreover, because the modelling concept is spatially explicit, I can use the model to elaborate on questions about how specific landscape properties affect communities. Both issues will be addressed in Chapter 3: in addition to mammal communities the model will also be applied to simulate bird communities. Furthermore, for the communities of both taxa, the complex effects of habitat loss and fragmentation, plus their combination, will be examined in detail. Here, particular focus will be given on taxon-specific space use characteristics and shifts in the competition regime within the communities.

Chapter 3

Habitat loss and fragmentation affecting mammal and bird communities – the role of interspecific competition and individual space use

---

A version of this chapter is submitted to *Ecological Informatics* as: Buchmann, C. M., Schurr, F. M., Nathan, R. and Jeltsch, F. Habitat loss and fragmentation affecting mammal and bird communities – the role of interspecific competition and individual space use.

3.1 Abstract

Fragmentation and loss of habitat are major threats to animal communities and are therefore important to conservation. Due to the complexity of the interplay of spatial effects and community processes our mechanistic understanding of how communities respond to such landscape changes is still poor. Modelling studies have mostly focused on elucidating the principles of community response to fragmentation and habitat loss at relatively large spatial and temporal scales relevant to metacommunity dynamics. Yet, it has been shown that also small scale processes, like foraging behaviour, space use of individuals and local resource competition are important. However, most studies that consider these smaller scales are designed for single species and are characterized by high model complexity. Hence, they are not easily applicable to ecological communities of interacting individuals. To fill this gap, we apply an allometric model of individual home range formation to investigate the effect of habitat loss and fragmentation on mammal and bird communities, and, in this context, to illuminate the role of interspecific competition and individual space use. Results show a similar response of both taxa to habitat loss. Community composition is shifted towards higher frequency of relatively small animals. The exponent and the 95%-quantile of the individual size distribution (ISD) of the emerging communities show threshold behaviour with decreasing habitat area. Fragmentation *per se* has a similar and strong effect on mammals, but not on birds: ISDs of bird communities were insensitive to fragmentation at the small scale considered here. These patterns can be explained by competitive release taking place in interacting animal communities, with the exception of bird buffering response to fragmentation, presumably by adjusting (and more specifically increasing) the size of their home ranges. These results reflect consequences of higher mobility of birds compared to mammals of the same size and the importance of considering competitive interaction, particularly for mammal communities, in response to landscape fragmentation. Our allometric approach enables scaling up from individual physiology and foraging behaviour to terrestrial communities, and disentangling the role of individual space use and interspecific competition in controlling the response of mammal and bird communities to landscape changes.

3.2 Introduction

The ongoing destruction and subsequent fragmentation of habitat are considered among the greatest contributors to recent and potential future extinctions (Fahrig 2003, Ewers and Didham 2006). While numerous studies have investigated in detail effects of landscape modifications on single species (Debinski and Holt 2000) or functional types (Körner and Jeltsch 2008, Körner et al. 2010, Jeltsch et al. 2011), the complex interplay of mechanisms affecting interacting animal communities at small scales like individual foraging behaviour or resource competition, is still poorly understood.

Even though differences in methodology and terminology in various studies cause difficulties to synthesise general conclusions (Fahrig 2003), effects of reduced habitat area (habitat loss) on populations are relatively consistent among studies and rather well understood. A large number of studies report threshold behaviour (so called ‘extinction thresholds’) of animal populations with reduced amount of habitat, and several theoretical modelling studies have proposed different mechanistic explanations for such non-linear dynamics, ranging from percolation theory and isolation effects to time lag and Allee effects (Bascompte and Solé 1996, Harrison and Bruna 1999, Fahrig 2002, Swift and Hannon 2010). In contrast, reported effects of fragmentation *per se* on populations are mostly weaker and often contradictory. Fragmentation *per se* here means the spatial configuration of habitat only while total habitat area remains unchanged (this aspect was also intensively discussed in the ‘SLOSS debate’, e.g. Wilcox and Murphy (1985) and references therein). Different studies report positive or negative effects of fragmentation on populations, but some also report no effect (Fahrig 2003, Smith et al. 2011). Particularly the interplay of habitat fragmentation with habitat loss (for example how fragmentation affects the threshold behaviour with habitat loss, or how total habitat area controls the strength of the fragmentation effect) still poses a hard challenge to scientists and conservation managers.

Interspecific interactions even enhance the complexity of system behaviour in response to landscape modifications in animal communities (Nee and May 1992, Debinski and Holt 2000, Banks et al. 2007, Brown 2007). Empirical investigation of such complex systems is difficult and most studies are therefore limited to either focus on abundance of single species (that means they miss the community context) or to species richness of communities (that means they miss information on the condition of the different populations) (Debinski and Holt 2000). Various modelling approaches have been developed to address and disentangle different mechanisms which control how populations in communities or complete communities respond to habitat loss and fragmentation. The vast majority of these models can be categorized in the family of metacommunity models (e.g. Leibold et al. 2004, Hawkes 2009; for more detailed description and categorization of different models see for example Kareiva et al. 1990, Flather and Bevers 2002, Swift and Hannon 2010). Metacommunity models work at large spatial and temporal scales and focus on dispersal as the crucial spatial process affected and constrained by landscape configuration.

Processes at small scales, such as foraging behaviour and movement, space use and local resource competition, however, play a crucial role in how individuals and species in interacting communities cope with heterogeneous resource distributions (Nee and May 1992, Ritchie 1998, Debinski and Holt 2000, Hawkes 2009, Gautestad and Mysterud 2010, Morales et al. 2010, Pita et al. 2010, Smith et al. 2011, Buchmann et al. 2011b). Different space use behaviour of individuals of different taxa – for example the higher mobility and larger home ranges of birds compared to mammals (Ottaviani et al. 2006, Breitbach et al. 2010) – can also affect the response of communities to changes in resource distributions. Nevertheless, theoretical studies investigating such small scale mechanisms (for example optimal foraging behaviour like Nonaka and Holme 2007, Skorka et al. 2009, but also Gautestad and Mysterud 2010) have generally not made the step to consider species interactions, implying they are not yet set to explore and resolve community questions. The main reason might be that studies accounting for the importance of individual behaviour and space use are too complex (Nonaka and Holme 2007, Van Moorter et al. 2009) and often designed for a specific single species (e.g. Bowers et al. 1996b, Skorka et al. 2009). We have recently proposed a simple alternative, an individual-based spatially explicit model of individual home range formation of multiple mammal species parameterized by allometric relationships (Buchmann et al. 2011a,b). This approach considers the important role of individual space use and resource competition on home range formation (e.g. Swihart et al. 1988, Nee and May 1992, Pita et al. 2010), thereby enabling mechanistic investigation of the processes structuring animal communities.

In this study we use this model (specifically a modification of the model described in Buchmann et al. (2011b), see Methods for details) to elaborate the role of interspecific competition and individual space use for communities facing landscape changes. Besides the application for mammals we here also paramterize the model for the first time for birds and explore how not only habitat loss, but also habitat fragmentation and the combination of both, affect the body mass distribution of these communities.

3.3 Methods

Our modelling study aims at exploring the response of the body mass distribution – namely the individual size distribution (ISD) (after White et al. 2007) – of mammal and bird communities to habitat loss and fragmentation, emphasising the role of interspecific competition and individual space use in particular. In the methods section we first explain the generation of simulation landscapes (including loss and fragmentation of habitat) followed by a brief description of the allometric model of home range formation for mammals and birds consuming primary production (i.e. herbivores and primarily herbivorous omnivores) and a description of how we use it to model community assembly. Here, we use a modification of the original model of Buchmann et al. (2011a), namely a slightly more complex submodel for the calculation of movement cost. Originally we introduced this modification in a study that focussed particularly on the effects of different assumptions on movement strategies for communities (Buchmann et al. 2011b; the submodel named 'body mass dependent nomadic movement model' BNF). This movement model was chosen here because it additionally considers body mass dependence of movement distances, is therefore more closely oriented towards movement data, and hence, seems more appropriate for the investigation of communities with a large range of body mass. For detailed model descriptions we refer the reader to the original sources.

3.3.1 Simulation landscapes

The well established and tested midpoint displacement algorithm (Saupe 1988, Hargrove et al. 2002, Körner and Jeltsch 2008, Jeltsch et al. 2011) was used to create fractal landscapes (257 × 257 cells, each interpreted as 10 m × 10 m, resulting in landscapes of ~ 6.6 km^2). With this approach landscape fragmentation can be controlled by the Hurst-factor H, describing the spatial-autocorrelation of grid cell values, interpreted as biomass productivity (Fig. 3.1). In simulations we used $H = 0.1$ for strongly fragmented, $H = 0.5$ for intermediate and $H = 0.9$ for weakly fragmented resource landscapes (σ^2, the variance in displacement of points, was set to 0.3 for all scenarios). To simulate habitat loss, grid cells with the lowest values, interpreted as resource productivity, were then set to 0 until a certain share of habitat S was left as productive (i.e. suitable) habitat (Fig. 3.1). In simulations S was set to 1.0, 0.75, 0.5, 0.3, 0.1 and 0.05. To guarantee for comparability between scenarios and avoid landscape artefacts, landscapes were rescaled using a rank-based transformation in order to achieve that all landscapes had the same normal distribution of grid cell values (mean and S.D.) as the landscapes with $S = 1.0$. Additionally all landscapes were scaled to have an average resource productivity in productive cells of 6.85×10^{-2} kg dry biomass × grid $cell^{-1}$ × day^{-1}, a value oriented towards the productivity of typical shrub lands and grasslands (Whittaker 1975). Only 20% of this primary production is assumed to be available to the mammal or the bird community considering competition with other taxa and because not all plant material is consumable (see Buchmann et al. 2011a for systematic variation of this value). The resource is, however, not further specified, hence we model a simplified community in which all individuals consume and compete for this single type of resource.

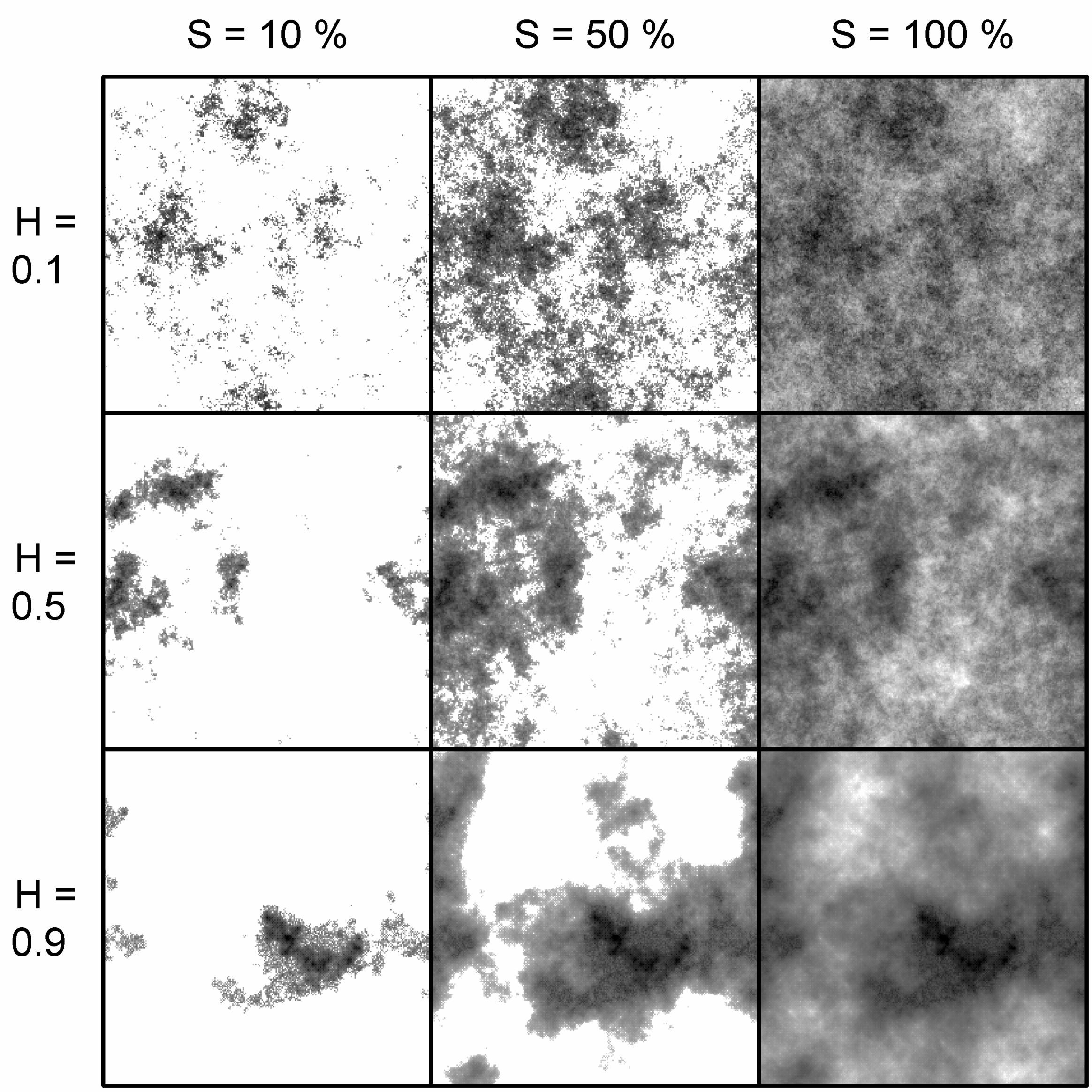

Figure 3.1. Illustration of exemplary simulation landscapes (257 × 257 grid cells) with different amount of suitable habitat S (habitat loss) and different levels of fragmentation (Hurst-factor H). Grey scale values represent the daily biomass production in a grid cell (from ~ 0.1 (light grey) to ~ 30 (black) g dry biomass).

3.3.2 Model of individual home range formation of mammal and birds

For individuals, whose body mass is drawn from a continuous distribution (see below), the model performs a search of the most efficient home range. This approach is based on optimal foraging theory (Mitchell and Powell 2004) and assumes that home ranges are circular and controlled by resource availability (Said and Servanty 2005). For the search of a home range all suitable grid cells are tested in random order as potential central home range ('core') cells. All grid cells in surrounding this possible core are checked with increasing distance (assuming periodic boundary conditions) for their potential to supply the animal with food. This daily resource supply of each grid cell is balanced with the costs that have to be spent on daily average for movement in order to calculate the effective resource gain from this cell. Movement costs related to the addition of a new grid cell to the potential home range of an individual are here calculated as the ratio between average daily movement distance and average home range size (measured in grid cells) of an individual. Doing so assures that the total costs for the sum of all home range cells correspond approximately to data on individual daily movement distance. Both, average movement distance and average home range size are derived from empirical allometric relations (see below and Buchmann et al. 2011b).

If enough resources can be achieved to cover the individual's daily resource requirements without the necessary area exceeding either the landscape size or a mass-specific maximum home range size, the search is considered successful. After testing all suitable cells as potential core cells, and if at least one of these searches was successful, the animal chooses the smallest, i.e. the most efficient, home range. Figure 3.2 illustrates principles of the individual home range search and how it leads to a community of interacting individuals with overlapping home ranges in space.

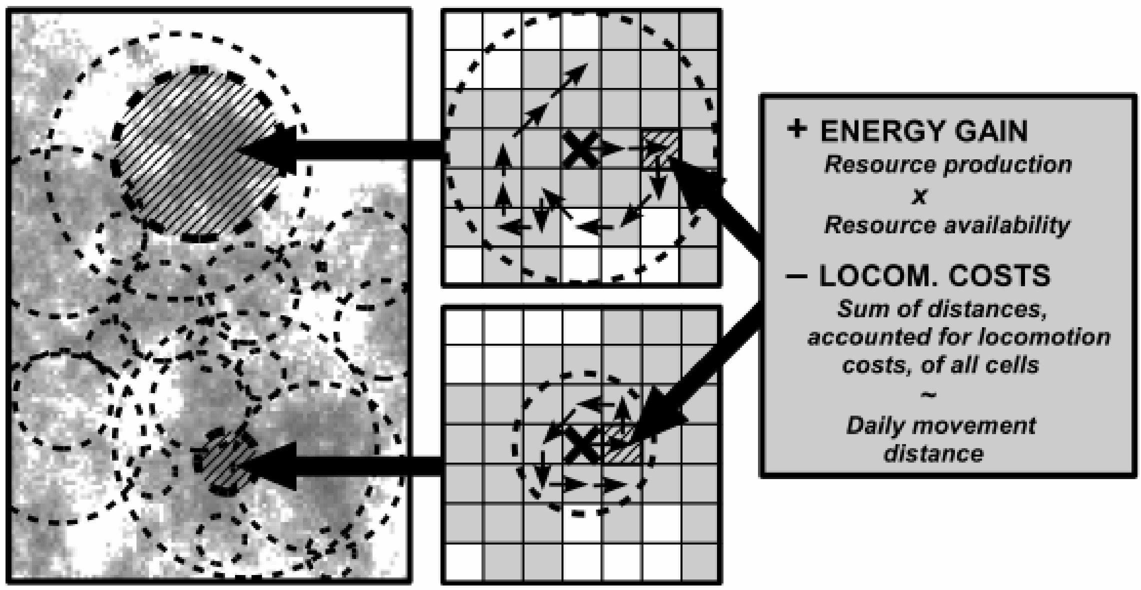

Figure 3.2. Schematic illustration of major model mechanisms of the allometric community model of individual home range formation. On the left, a section of a simulation landscape with some overlapping home ranges is shown (resource productivity is indicated as grey scale values, home ranges as circles). For two of these home ranges (a small one of a small individual, and a larger one of a larger individual) exemplary movement paths are illustrated, which could be represented by the approach used to calculate movement costs (see text for details). Note that smaller animals visit a higher proportion of home range cells on a daily basis than do larger animals because daily movement distance scales with ~ 0.25, whereas home range size scales with ~ 1 with body mass. During the home range search the energy balance of each home range cell is calculated on a daily basis, as shown on the right side. Home ranges can be established if the resource requirements can be satisfied by the sum of all home range cells on a daily basis.

Since individuals are characterized by their body mass, all model parameters related to this model compartment can be parameterized by allometric relationships. Here only the sources and/or the derivation of used allometric relationships are given. For explicit equations for the bird model see Appendix 3.A; for mammals see Buchmann et al. (2011a) and, for the approach to calculate movement costs, see Buchmann et al. (2011b).

Daily energy requirement of individuals are determined after the allometric equations of field feeding rate for mammals and birds, given in Nagy (2001), and the locomotion cost per distance is calculated after equations reported by Calder (1996). For the calculation of the costs involved in adding new cless to a potential home range we need allometric relationships for daily movement distance and for average home range size (see above). For mammals we use an allometric relationship of daily movement distance for non-carnivorous mammals, reported by Garland (1983) (see Fig. 3.2). Comparable data on daily movement distance are, to our knowledge, not available for birds. Sutherland et al. (2000) found that the allometry of natal dispersal distance has the same slope for birds and mammals; the coefficient is, however, 10 times higher for birds. As a first approximation we assume that this result characterizes general differences in movement behaviour between mammals and birds (i.e. a generally 10 times higher mobility in birds) and we apply the mammal equation for daily movement distance multiplied by 10 for birds, as our yet-to-be-confirmed assumption. As estimate for average home range size we apply a combination of different empirically observed allometric relationships for birds and mammals (see Appendix 3.B for references). In order to then balance energetic costs of movement with resource use, these costs were converted into dry biomass equivalent by a factor given in Nagy (2001) for non-fermenting consumption of plant diet. The allometric relationship for maximum home range size for mammals is calculated as the combination of maxima of constraint spaces for home range size of herbivores and omnivores reported by Kelt and Van Vuren (2001). Since no comparable data is available for birds we re-analysed data from Ottaviani et al. (2006) on non-defended feeding areas of omnivorous birds (because omnivores generally have larger home ranges than herbivores, birds as well as mammals, e.g. Harestad and Bunnell 1979, Holling 1992, Ottaviani et al. 2006) using quantile regression (R package ‘quantreg’, R Development Core Team 2008, Koenker 2009) on log-transformed data. The back-transformed (antilog) equation corresponding to the 95%-quantile is used as an estimate of maximum home range size for birds.

The share of available resource productivity that can actually be exploited by an individual in a grid cell is also assumed and calculated to depend on body mass, scaling with an allometric exponent of -0.25. Such body mass dependence of individual resource availability or resource use efficiency has been invoked previously to explain the allometry of home range size (Harestad and Bunnell 1979, Holling 1992, Haskell et al. 2002, Jetz et al. 2004, Buchmann et al. 2011a). The coefficient of this allometric relationship γ_{PI}, determining the general magnitude of individual resource availability, is a model parameter (in simulations we use $\gamma_{PI} = 0.04$, a value that yielded realistic community structure for mammals and birds; for model validation and sensitivity analysis see Appendix 3.B).

3.3.3 Community assembly and analysis of simulation output

Body masses of mammal individuals are sequentially drawn from a truncated power law distribution between 0.005 and 100 kg, with an exponent of -1.5 (a value in the range tested by Buchmann et al. 2011a yielding realistic community structure). For physiological limits (Chatterjee et al. 2007, Rohwer et al. 2009), the upper body mass limit of birds was set to 20 kg. To compare effects of habitat loss and fragmentation, here mammal and bird communities were simulated separately. For each individual the search for an optimal home range is performed as described above. If the search was successful, resources are partly depleted within the home range about the amount available to the individual (see above) and the next animal is facing a landscape reduced in resources. In order to test for the effect of competition between different body mass ranges that could represent single populations, we also ran simulations where only smaller animal mass windows were allowed, yet drawn out of the same input distribution (mammals: 0.01-0.02, 3-5, 20-30 and 50-75 kg, birds: 0.01-0.02, 1-2, 3-5 and 12-18 kg).

Simulations were stopped when a certain share of community resources were consumed by the individuals, which reflects certain community saturation. To determine this specific resource level, the different scenarios were initially run until 5,000 individuals consecutively failed in establishing a home range. The amount of resources consumed by the community at this stage was then interpreted as 100% (full community saturation). This assumption is justified because even for much smaller number of consecutively failing animals the overall amount of consumed resources changed very little. Knowing the resource level corresponding to 100% community saturation then allowed us to stop each simulation at a defined community saturation (SAT) via the actual level of community resource consumption. Here we use SAT = 0.95, a value resulting in realistic communities (for sensitivity analysis of this model parameter see Appendix 3.B).

The major model output is the individual size distribution (ISD) of all individuals in the community which can be well described by a power law distribution (Buchmann et al. 2011a). We determined the exponent of this distribution using a maximum likelihood fit. Moreover the 95%-quantile of this distribution was calculated. The allometric relationship between body size and home range size predicted by the model was calculated by a linear regression of log-transformed data (Buchmann et al. 2011a). For the analysis of competition between different smaller ranges of body mass (interpreted as populations, see above), the number of individuals of these populations was determined.

3.4 Results

The distribution of individual body mass (ISD) shows a strong response to habitat loss (less suitable habitat area S) and fragmentation (spatial configuration of remaining habitat, controlled by the Hurst-factor H), however, differently for mammal and bird communities (Fig. 3.3a, b and c, d, respectively). For both taxa, habitat loss of up to 25% (100% to 75% suitable habitat area) does not significantly alter the ISD distribution (indicated by the ISD exponent) or the size of the largest individuals (indicated by the 95%-quantile of body mass) in the community. The zone of relatively low impact extends to ~ 70% habitat loss in birds, but not in mammals. This is particularly notable in mammal communities in highly fragmented landscapes (H = 0.1), which shift to higher frequency of relatively small animals (Fig. 3.3a and c), and to a reduced size of the largest individuals in the community (Fig. 3.3b and d). This shift, occurring at more severe cases of habitat loss also in bird communities, exhibits non-linear threshold behaviour with increasing habitat loss, but more profoundly in mammals than in birds. Fragmentation *per se* (i.e. the same habitat area) hardly has any effect on the response to habitat loss in bird communities; mammal communities, however, exhibit strong response. With increasing fragmentation, the ISD exponent as well as the 95%-quantile of body mass in mammal communities are reduced at relatively low levels of habitat loss, and the reduction of both variables by fragmentation is stronger under higher levels of habitat loss.

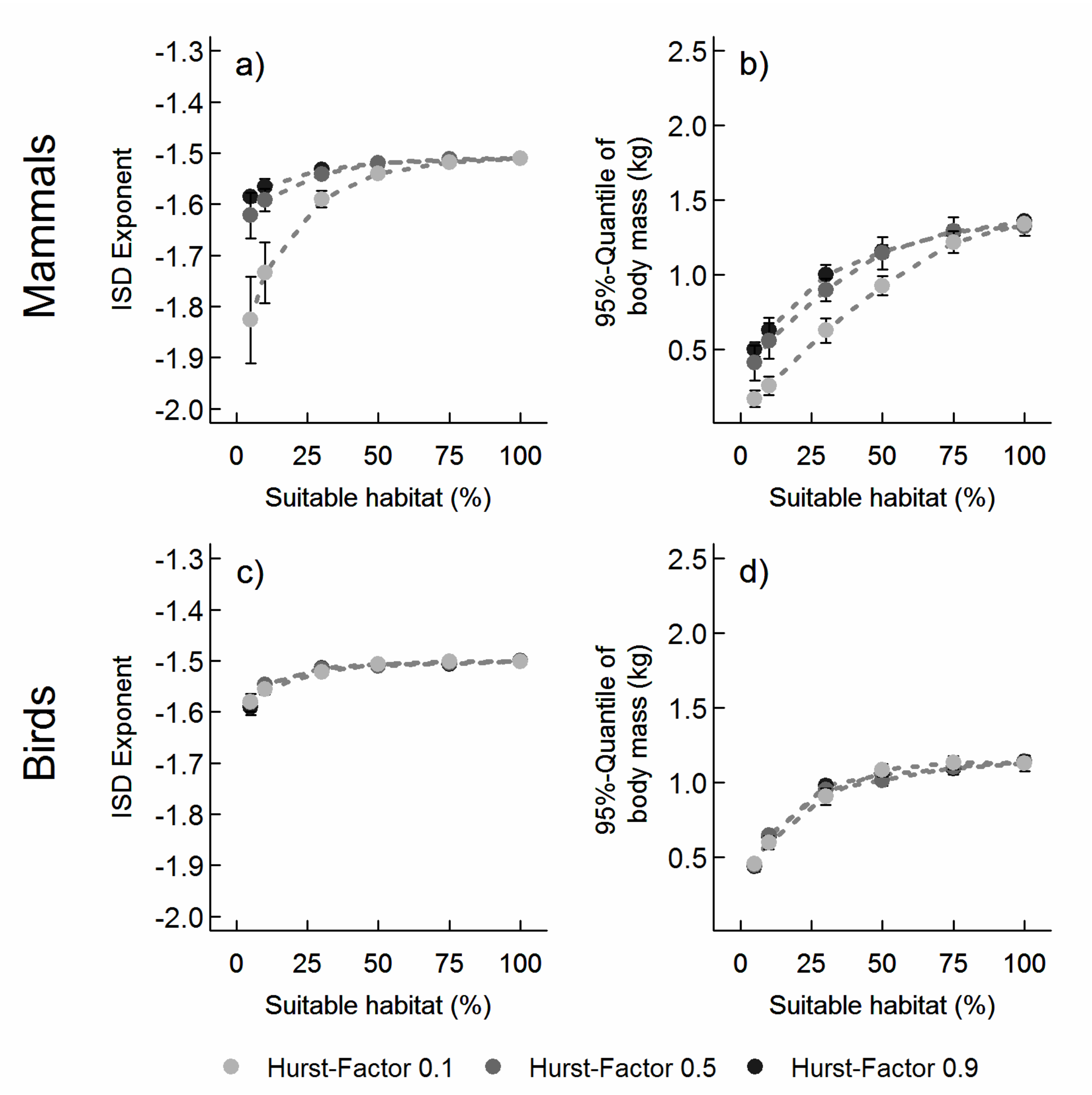

Figure 3.3. Effect of habitat loss and fragmentation on the community body mass distribution, specifically the individual size distribution ISD. Changes of the exponent (a and c) and of the of the 95%-quantile (b and d) of this distribution are shown for mammal (a and b) and bird (c and d) communities. Symbols are the means, error bars the 95% C.I.s of five landscape replicates. Grey scale values symbolize landscape fragmentation, see legend.

The basic effects of habitat loss, i.e. less suitable habitat area, on the community body mass distribution can be explained by taking a closer look at narrower mass windows of the mammal community (Fig. 3.4a-d). Such smaller body mass ranges could be interpreted to represent populations of single species and are therefore hereafter referred to as ‘populations’ for better readability. The size of these populations decreases with habitat loss, however, the reduction of abundance deviates considerably from a linear decrease (this can be well seen when only this deviation is illustrated, Fig. 3.4e-h). The largest species is affected strongly already when still 75% habitat is available and the abundance is below the abundance corresponding to a linear decrease for all levels of habitat area. When each mass class (population) is simulated in isolation, so that there is no competition with the other body masses outside this mass class (other species), also smaller species show this response to habitat loss (Fig. 3.4i-l). However, when simulated together with the entire community, (i.e. under interspecific competition), the smaller species even profit from habitat loss, relative to the linear decrease of abundance. There is the trend that for smaller species the range of suitable habitat levels with which a species 'profits' is shifted to less habitat (Fig. 3.4e-g). These findings reflect the role of competition in explaining the non-linear response of the ISD exponent and the different thresholds in the response of the exponent and the 95%-quantile of the ISD. For birds these patterns are similar (see Fig. 3.C.1, Appendix 3.C).

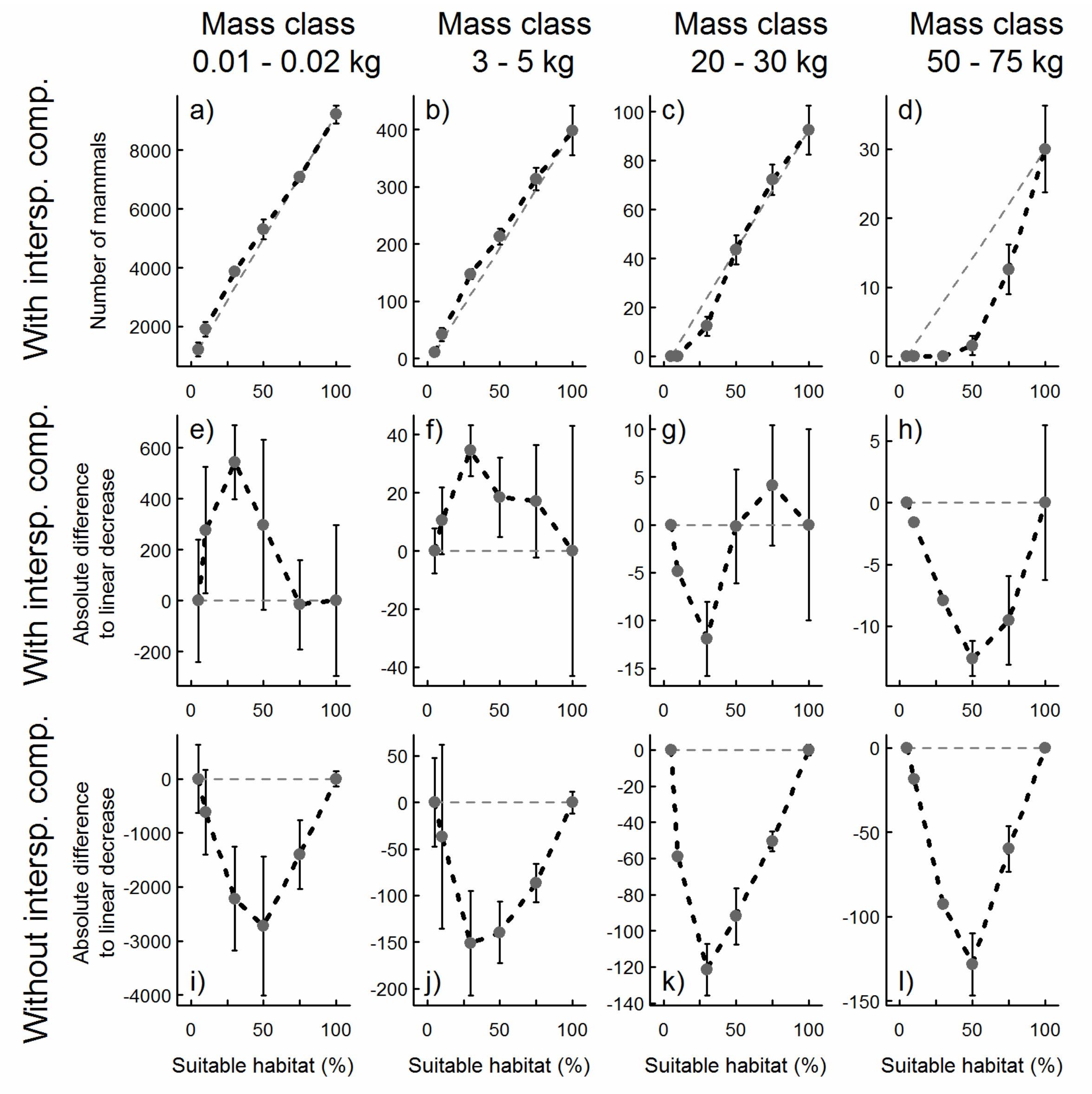

Figure 3.4. Effect of habitat loss on the number of mammals in narrower mass ranges (representing populations of certain species). Population size of these populations in mammal communities is shown in dependence of the amount of suitable habitat (a-d). The thin dashed lines connect the population size at highest and lowest habitat area, i.e. they denote a linear decrease of population size with habitat loss. The deviation of population size from this linear decrease is shown in the middle row (e-h). Below (i-l), the deviation from a linear decrease of population size with habitat loss for simulations of the populations alone, i.e. without competition with individuals outside the respective mass range, is shown. Grey symbols show the means, error bars the 95% C.I.s of five landscape replicates with intermediate fragmentation (H = 0.5).

In contrast to habitat loss, which has a similar effect on mammal and bird communities, fragmentation disproportionately affect mammals compared to birds (Fig. 3.3a and b). The importance of interspecific competition for the observed strong effect of fragmentation on mammal communities can be demonstrated by considering a population of small mammals (0.01-0.02 kg) at different levels of fragmentation. When this population is simulated alone, i.e. without interspecific competition, fragmentation decreases population size (Fig. 3.5a). This effect is rather weak, yet strongest at 30% suitable habitat. However, if the response of this population is observed in the community context (i.e. simulated together with all other body masses, and hence with interspecific competition) the effect of fragmentation is reversed, and stronger relative to population size (Fig. 3.5b). Now, the abundance of this small-bodied population is increased with increasing fragmentation, the most at 15% suitable area.

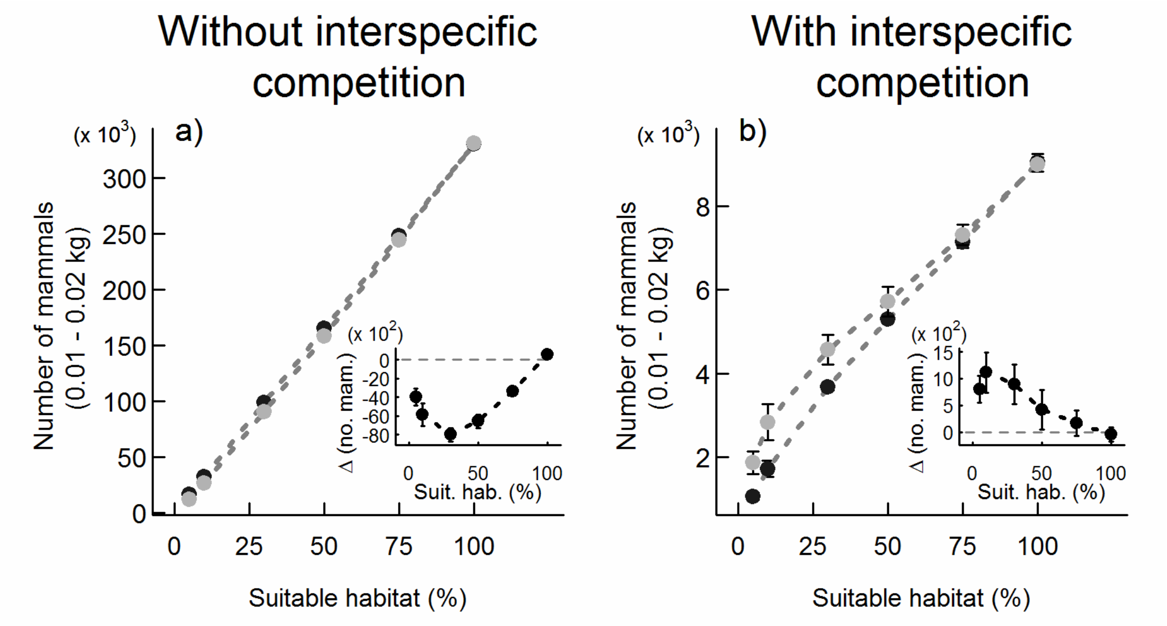

Figure 3.5. Effect of habitat loss and fragmentation on the number of mammals in a smaller body size range (0.01-0.02 kg), that could represent a population of a small-bodied species, at different levels of suitable habitat. The population is simulated alone (a) and in competition with the entire mammal community (b). Symbols show the means, error bars the 95% C.I.s of five landscape replicates. Grey scale values symbolize landscape fragmentation: light grey for strongly fragmented (H = 0.1) and black for weakly fragmented (H = 0.9) habitat. Inserts show the absolute difference between the number of animals in strongly and weakly fragmented landscapes, i.e. the ‘absolute fragmentation effect’.

In order to explain the differences in fragmentation effects between mammals (strong fragmentation effect on the ISD, particularly with little habitat area) and birds (hardly any fragmentation effect on the ISD), we compare the relative fragmentation effect on two populations (specifically mass ranges from 0.01 to 0.02 kg and from 3 to 5 kg) of both taxa in the community context, i.e. with interspecific competition. In both mammals and birds, the relative effect of fragmentation on population size is largest for the lowest habitat area tested (5%) and approaches 0 with increasing habitat area (Fig. 3.6). Populations of heavier mammal and bird species (Fig. 3.6b and d, respectively) show a comparable response, namely a negative effect of fragmentation on population abundance. While for mammals this effect is strong (increase of abundance by more than 90%), it is remarkably weaker for birds (less than 40% with high variation). The small-bodied bird species also suffers from fragmentation when little habitat area is available (Fig. 3.6c), comparable to the large-bodied bird species, but the effect is even much weaker (~ 10%). However, for the small-bodied mammal population fragmentation has a positive effect: it increases the abundance up to more than 70% (Fig. 3.6a).

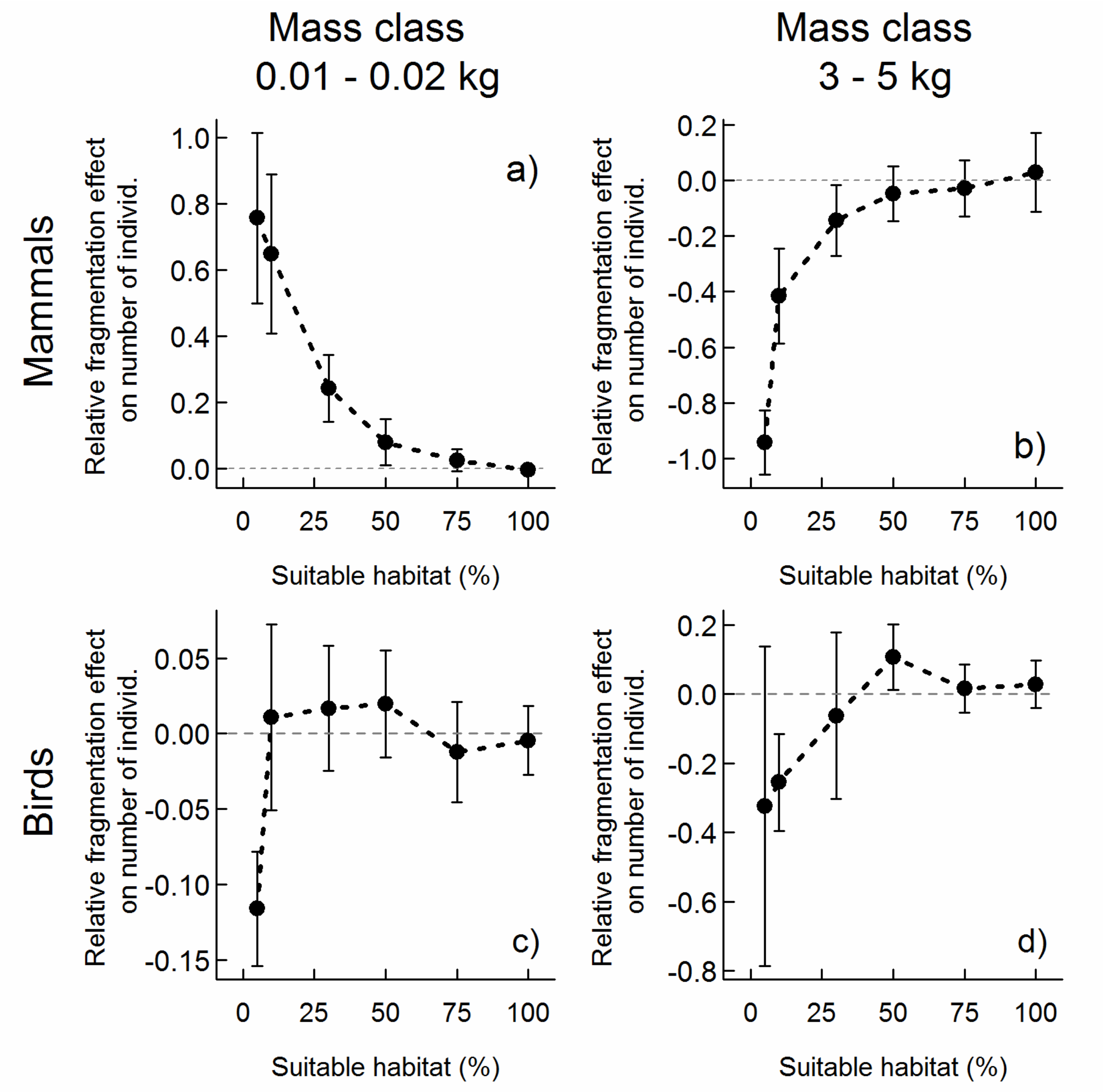

Figure 3.6. 'Relative fragmentation effect' on mammal and bird populations with interspecific competition. The relative fragmentation effect is the relative difference between the number of individuals in strongly and weakly fragmented landscapes ((#(H = 0.1) – #(H = 0.9)) / #(H = 0.9)), here shown for two body size ranges (0.01-0.02 and 3-5 kg), representing single populations in either mammal (a and b) or bird (c and d) communities. Symbols show the means, error bars the 95% C.I.s of five landscape replicates.

The allometry of home range size in simulated communities also shows a different response to decreasing suitable habitat (habitat loss) and fragmentation between mammals and birds (Fig. 3.7a and b compared to c and d). The allometric exponent increases slightly with habitat loss which indicates that larger animals more strongly increase their home range size than smaller animals. This response is slightly stronger for birds (compare Fig. 3.7a and c). The allometric exponent also increases with increasing habitat fragmentation. This fragmentation effect is particularly strong in bird communities and decreases with increasing suitable habitat. A similar pattern can be seen regarding the allometric coefficient (i.e. the average home range size of a 1 kg animal) (Fig. 3.7b and d). This indicates that birds generally react much stronger to a combination of habitat loss and fragmentation by increasing home range sizes than do mammals.

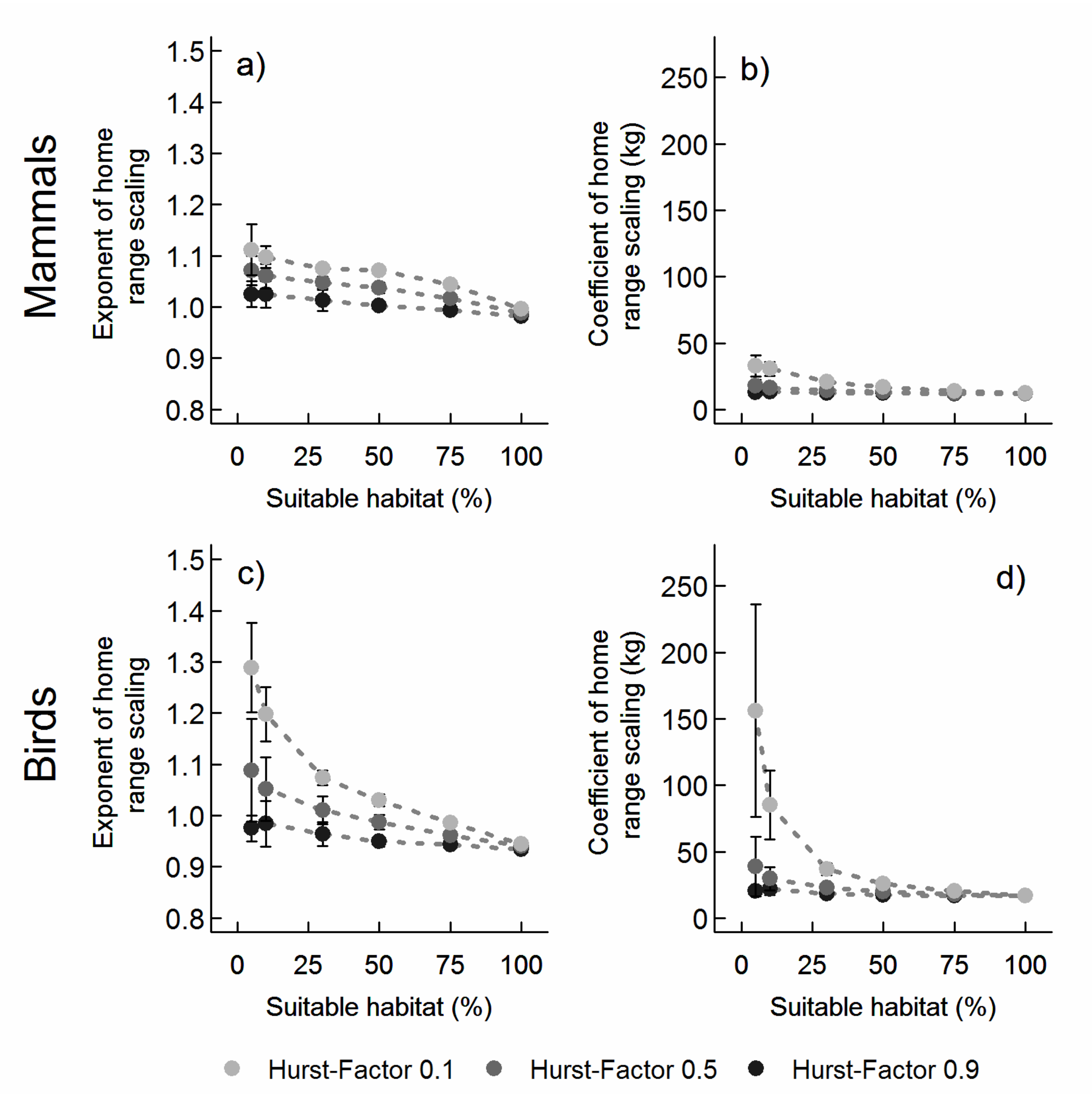

Figure 3.7. Effect of habitat loss and fragmentation on the parameters of the allometry of home range size of the mammal (a and b) and bird (c and d) communities. Allometric coefficients are given for body mass in kg and home range size in ha. Symbols show the means, error bars the 95% C.I.s of five landscape replicates. Grey scale values symbolize landscape fragmentation, see legend.

3.5 Discussion

To our knowledge, we challenged here for the first time the task of explaining how habitat loss and fragmentation affect the individual size distribution (ISD) of mammal and bird communities in terrestrial systems. In contrast to aquatic systems, the mechanisms that control body mass distributions, and how these mechanisms are affected by environmental change, are still largely unexplored in terrestrial communities (White et al. 2007). Our mechanistic model of individual home range formation in animal communities enables explicit exploration of the role of two important small scale mechanisms – individual space use and resource competition – in controlling the response of mammal and bird communities to habitat loss and fragmentation.

3.5.1 Effects of habitat loss on mammal and bird communities

Model predictions with respect to habitat loss (less suitable habitat area) agree for mammals and birds in demonstrating a shift to higher frequency of smaller and lower frequency of larger individuals. This is reflected in steeper ISDs (more negative exponents) and smaller size of the largest individuals in the community (smaller 95%-quantile). Higher vulnerability of larger individuals to habitat loss has been reported in previous studies and was often related to their lower abundance (Belovsky 1987, Gaston and Blackburn 1996, Harrison and Bruna 1999, Ewers and Didham 2006, but see Henle et al. 2004). The limitation of home range establishment of the individuals of a species is likely to be linked to the probability of local extinction of that species in the longer run. Hence, both the lower abundance and the higher extinction risk of larger animals are reflected in our simulation results.

The response of the ISD (exponent and 95%-quantile) shows, however, a non-linear response to habitat loss, namely only a strong reaction after some critical threshold of remaining habitat area has been reached. Critical (extinction) thresholds have been described and reviewed repeatedly in connection with habitat loss (e.g. Fahrig 2003, Swift and Hannon 2010). These thresholds typically range in similar magnitudes of habitat loss as those predicted by our model for the ISD exponent. The threshold response of the ISD exponent to habitat loss can be explained when observing different smaller mass windows (each presumably represents a different population) in the community. When large species decline in abundance or even ‘go extinct’ with decreasing habitat area, resources become available to (the next) smaller species. This species can therefore compensate some of the negative effects of habitat loss on their abundance. The ISD exponent thus initially remains fairly unaffected with decreasing habitat, even if the 95%-quantile already is reduced. This effect of competitive release (Thompson and Fox 1993, Larsen, Lopera and Forsyth 2008) resembles the phenomenon of mesopredator release reported for carnivores (Crooks and Soulé 1999) and could thus be termed ‘mesocompetitor release’. To our knowledge, this phenomenon has not yet been reported for herbivore communities, and its existence therefore remains to be tested for empirically. The effect that smaller individuals profit from the release of competition with larger individuals becomes mainly relevant for the smallest animals when less habitat area is available. This, in turn, explains the strong response of the ISD exponent (changing to more negative values, i.e. indicating a steeper ISD, with many small and very few large individuals) in the range of ~ 20% habitat area.

3.5.2 Effects of habitat fragmentation

In contrast to the effects of habitat loss, fragmentation *per se* (i.e. with constant habitat area) differentially affects mammal and bird communities. In accordance to previous studies our model predicts smaller effect of fragmentation, compared to habitat loss, on birds (Trzcinski et al. 1999, Smith et al. 2011). Community composition, reflected by the ISD, is not influenced by spatial configuration of habitat patches. In contrast, the allometry of home range size in bird communities strongly responds to fragmentation. This result seems reasonable considering the generally higher mobility of birds (Sutherland 2000, Ottaviani et al. 2006, Breitbach et al. 2010). The more plastic home range behaviour of birds enables them to buffer fragmentation effects on population abundance, for instance by enlarging home range size to include more isolated resource patches. This has been reported previously as ‘expansion response’ and was observed in bird populations (Ims et al. 1993). In our model communities this mechanism allows individuals to establish a home range in spite of unfavourable conditions (strong fragmentation) and might therefore be able to prevent species from extinction.

In mammal communities home range scaling is considerably less sensitive to fragmentation than in bird communities (compare McCann and Benn 2006, Said et al. 2009, but see Selonen et al. 2001). This indicates their weaker potential to buffer fragmentation effects on community composition via individual space use. In turn, mammals react more strongly by decreasing abundance or even going extinct, particularly when also only little habitat area is available. Consequently, competitive release also becomes the relevant mechanism controlling mammal community response to fragmentation (as it is for the effect of habitat loss). We have shown that a population of very small mammals suffers from fragmentation in the absence of interspecific competition, comparable to the findings of a conceptual study not considering species interactions (Flather and Bevers 2002). However, in the presence of interspecific competition such a population might even benefit from fragmentation. This positive effect of fragmentation is again explained by a disproportionally stronger negative effect of fragmentation on larger mammals, which decrease in abundance, causing competitive release of smaller mammals.

3.5.3 Model shortcomings and future directions

Our study considers small scale fragmentation at the scale of foraging areas (according to Smith et al. 2011). Large scale fragmentation can of course cause additional effects that we did not address. Isolation, for example, might affect small individuals in particular (Flather and Bevers 2002, Brown 2007). Moreover, factors related to population dynamics, like longer life span of larger animals or faster recovery related to shorter generation times of smaller individuals (Wissel et al. 1994), are not considered in our framework. One could also expect the higher energy expenditure of birds in larger home ranges in fragmented landscapes to decrease reproductive output (Hinsley 2000). Other factors that are important to be considered for effective conservation planning are matrix (Prugh et al. 2008) and edge effects – the latter particularly for birds that often suffer from increasing nest predation rates at edges of habitat patches (Fletcher et al. 2007, Lindell et al. 2007). The combination of these possible additional factors could also cause behavioural changes such as increased territoriality (Ims et al. 1993, Banks et al. 2007). This complexity of factors and mechanisms demonstrates that our results cannot resolve the complete story of community response at all relevant scales. However, we have for the first time investigated and demonstrated the relevance of small scale mechanisms at the individual level for terrestrial communities experiencing landscape changes. Promising future steps should therefore combine large scale metacommunity models with individual-based modelling of relevant small scale mechanisms, like our optimal foraging based home range approach (see also Hawkes 2009). For more accurate model design and validation of predicted patterns, appropriate data at the community scale are required. In particular, multi-species abundance data for communities in differently fragmented habitats and more refined movement data in general and for estimating the allometry of daily movement distance in particular seem to be of high importance.

3.6 Conclusion

Using allometric relationships to combine resource competition and space use, considering individual physiology and foraging behaviour, our model predicts both common and distinct patterns of community response to habitat loss and fragmentation for mammals and birds. Our results imply that mammals are particularly sensitive to a combination of habitat loss and habitat fragmentation, whereas birds are strongly affected only by habitat loss and can compensate for the negative effects of fragmentation by flexible individual space use enabled by their higher mobility. In the context of the SLOSS debate (Wilcox and Murphy 1985 and references therein) our results suggest taxon-specific differences: while mammals depend on large patches (SL), birds can also cope with many small patches (SS). Particularly for mammals, competitive release in interacting communities was shown to possibly reverse landscape effects on single species. Overall, we propose an allometric approach to address the challenging scaling-up problem of linking individuals to communities, and, more specifically, highlight the importance of considering the role of movement capacity of individuals and interspecific competition in shaping animal response to habitat loss and fragmentation.

3.7 Appendix 3.A – Methodological details of the home range model

Allometric equations for resource requirements, specific locomotion costs and maximum home range size used to parameterize the model for mammals are given in Buchmann et al. (2011a) and for the movement model for mammals in Buchmann et al. (2011b). As resource requirement for birds we use the allometry of field feeding rate given in Nagy (2001):

$$\mathrm{FR} = 0.072 \times \mathrm{M}^{0.69} \qquad \text{(kg dry biomass} \times \text{day}^{-1}\text{, M in kg).} \qquad (3.\mathrm{A}.1)$$

Locomotion costs per distance for birds are given in Calder (1996) as

$$\mathrm{L} = 5.23 \times \mathrm{M}^{0.77} \qquad (\mathrm{J} \times \mathrm{m}^{-1}\text{, M in kg).} \qquad (3.\mathrm{A}.2)$$

The 95%-qunatile of the quantile regression of data of non-defended feeding areas for omnivorous birds (from Ottaviani et al. 2006) yield the following allometric equation, which is used as maximum home range constraint for the bird model:

$$\mathrm{HR}_{\mathrm{max}} = 4457.38 \times \mathrm{M}^{1.22} \qquad \text{(ha, M in kg).} \qquad (3.\mathrm{A}.3)$$

To achieve that the sum of all effective distances (for all home range cells) which locomotion costs are ‘paid’ for on daily average, follow daily movement distances, the effective distance for each home range cell is calculated as the quotient of daily movement distance (DMD) and number of cells in the home range (HR). For birds we apply the following allometric equations:

$$\mathrm{DMD}_{\mathrm{bird}} = 8750 \times \mathrm{M}^{0.22} \qquad \text{(m, M in kg), and} \qquad (3.\mathrm{A}.4)$$

$$\mathrm{HR}_{\mathrm{bird}} = 19167 \times \mathrm{M}^{0.95} \qquad \text{(cells, M in kg).} \qquad (3.\mathrm{A}.5)$$

Equation 3.A.4 is the equation reported by Garland (1983) for non-carnivore mammals, multiplied by 10 (see Methods and Sutherland 2000). Equation 3.A.5 is obtained as a combination (the mean of coefficients and exponents) of reported allometric relationships for home range size (see Appendix 3.B).

3.8 Appendix 3.B – Validation and sensitivity analysis of the community model

Model predictions agree well with empirical data (see below) for the majority of parameter settings (Fig. 3.B.1 and 3.B.2). For simulations exploring the effect of habitat loss and fragmentation on communities we use values of the two major parameters that lead to good agreement between model and data (γ_{PI} = 0.04 and SAT = 0.95). Smaller γ_{PI}-values could be chosen for birds, and larger ones for mammals; for better comparability we decided to use the intermediate value. Model response to variation of these two model parameters are in detail discussed in Buchmann et al. (2011a).

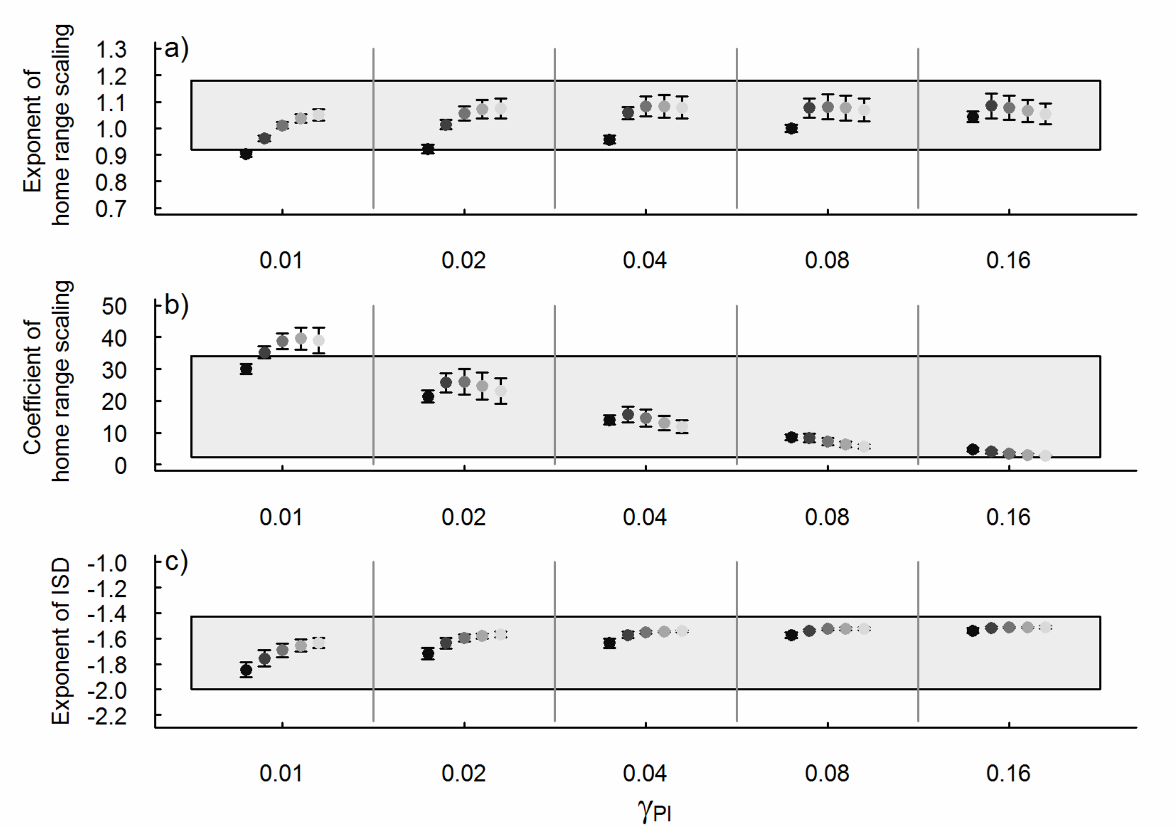

Figure 3.B.1. Validation and sensitivity analysis for the community home range model parameterized for mammals. Model results are shown for the three major model ouput variables characterizing the allometric scaling of home range size (a and b) and the individual size distribution of the community (c) in dependence of the two major model parameters γ_{PI} and SAT in medium fragmented landscapes (H = 0.5 and S = 0.15). Grey symbols show the means of five landscape replicates, error bars the 95% C.I.s. Grey scale values symbolize the SAT-values 0.99 (black), 0.95, 0.9, 0.85 and 0.8 (light grey). Grey boxes indicate the range of comparable empirical data (see text for details).

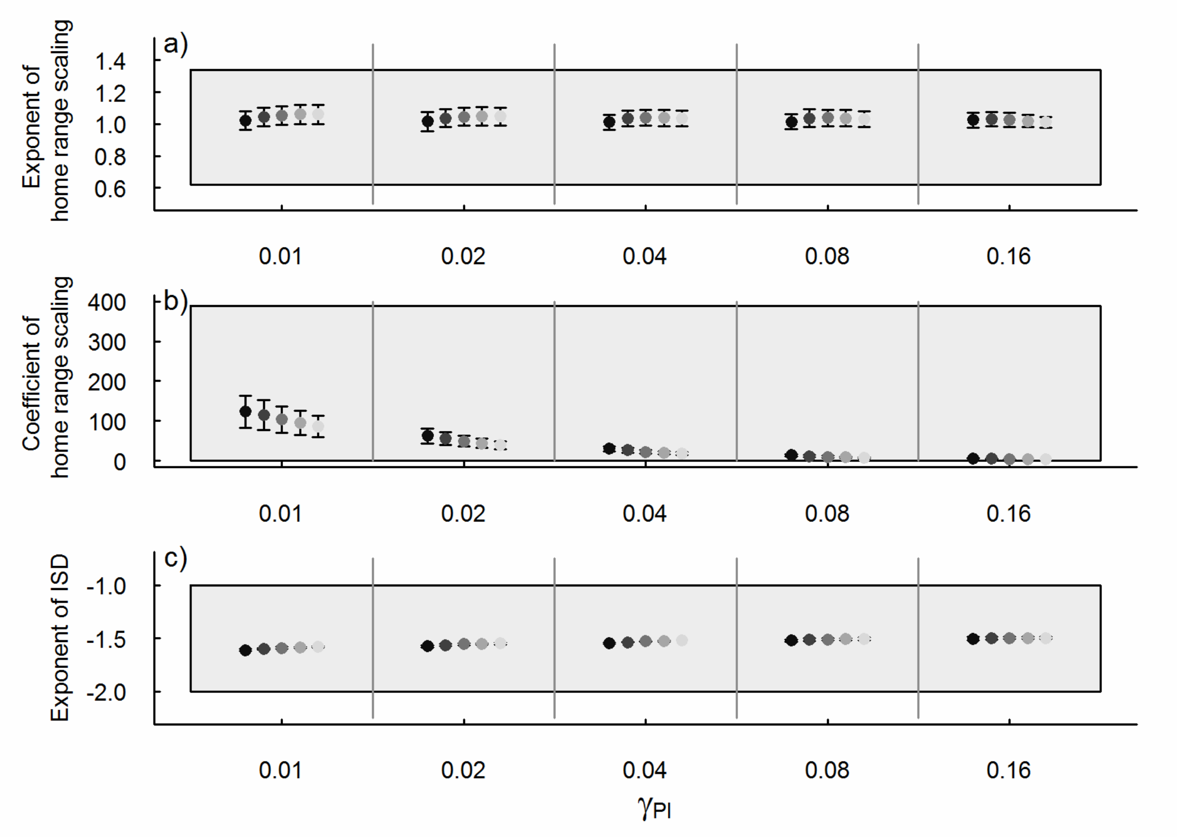

Figure. 3.B.2. Validation and sensitivity analysis for the community home range model parameterized for birds. Model results are shown for the three major model ouput variables characterizing the allometric scaling of home range size (a and b) and the individual size distribution of the community (c) in dependence of the two major model parameters γ_{PI} and SAT in medium fragmented landscapes (H = 0.5 and S = 0.15). For details see figure 3.B.1.

Data on the allometry of home range size for mammals, to which we compare model output (the grey boxes in Fig. 3.B.1), are taken from Harestad and Bunnell (1979) and Ottaviani et al. (2006) for herbivores and omnivores, and from Holling (1992) for herbivores. For birds the 'validation' boxes (Fig. 3.B.2) span the range of exponents and coefficients reported for the allometry of non-defended feeding areas of omnivorous birds (Ottaviani et al. 2006) and of breeding territories of non-migrant birds (Bowman 2003, carnivorous bird species were excluded before re-analysis). Since data quality for herbivorous birds does not allow proper analysis (Holling 1992, Ottaviani et al. 2006) and hence no values can be obtained from the literature, we follow Hollings (1992) argument that herbivores have around 20 times smaller home ranges than carnivores (while the exponent is not distinguishable), by taking the equation of Ottaviani et al. (2006) for non-defended feeding areas of carnivorous birds divided by 20, in order to get an approximation for herbivorous birds.

The validation range for the exponent of the individual size distribution (ISD) of mammal communities is based on theory and data of Burbidge and McKenzie (1989), Brown and Nicoletto

(1991) and Brown (1995) (for exact derivation of values see Buchmann et al. 2011a). Like in mammals, also in local bird communities, the distribution of mean species body mass follows approximately a log-uniform distribution, i.e. a power law distribution with an exponent of -1 (Blackburn and Gaston 1994, Brown 1995). The relationship between body size and population density in birds is, however, not as distinct as in mammals. While this relationship is described to (theoretically and practically) be characterized by a scaling exponent between -0.75 and -1 (Brown 1995), exponents reported span values from -0.09 to -0.98 (Peters 1983, Blackburn et al. 1993, Cotgreave 1993, no relationship found: Cotgreave and Stockley 1994). Combining these two relationships (of the distribution of species body size and the allometry of species abundance in analyogy to Buchmann et al. 2011a), yields a range of expected values approximately between -1 and -2.

3.9 Appendix 3.C – Additional results of the response of bird populations to habitat loss

Figure 3.C.1 shows the effect of habitat loss on bird populations, specifically small mass windows that could represent single populations (equivalent to Fig. 3.4e-l, showing corresponding results for mammals). Like mammals (Fig. 3.4i-l), all bird populations suffer from habitat loss, relative to linearly decreasing population size with habitat loss (indicated by the horizontal dashed line) if simulated alone (Fig. 3.C.1e-h), that means without interspecific competition. If the same populations are simulated in the community (with competition with individuals outside the respective mass window), only the largest species clearly suffers (Fig. 3.C.1d), whereas smaller species even ‘profit’, relative to the linear decrease (Fig. 3.C.1a-b). These patterns are comparable to those observed for mammals, even if in mammals they are slightly more pronounced and characterized by lower variability, which is also reflected in clearer patterns of mammal ISD response to habitat loss (Fig. 3.3).

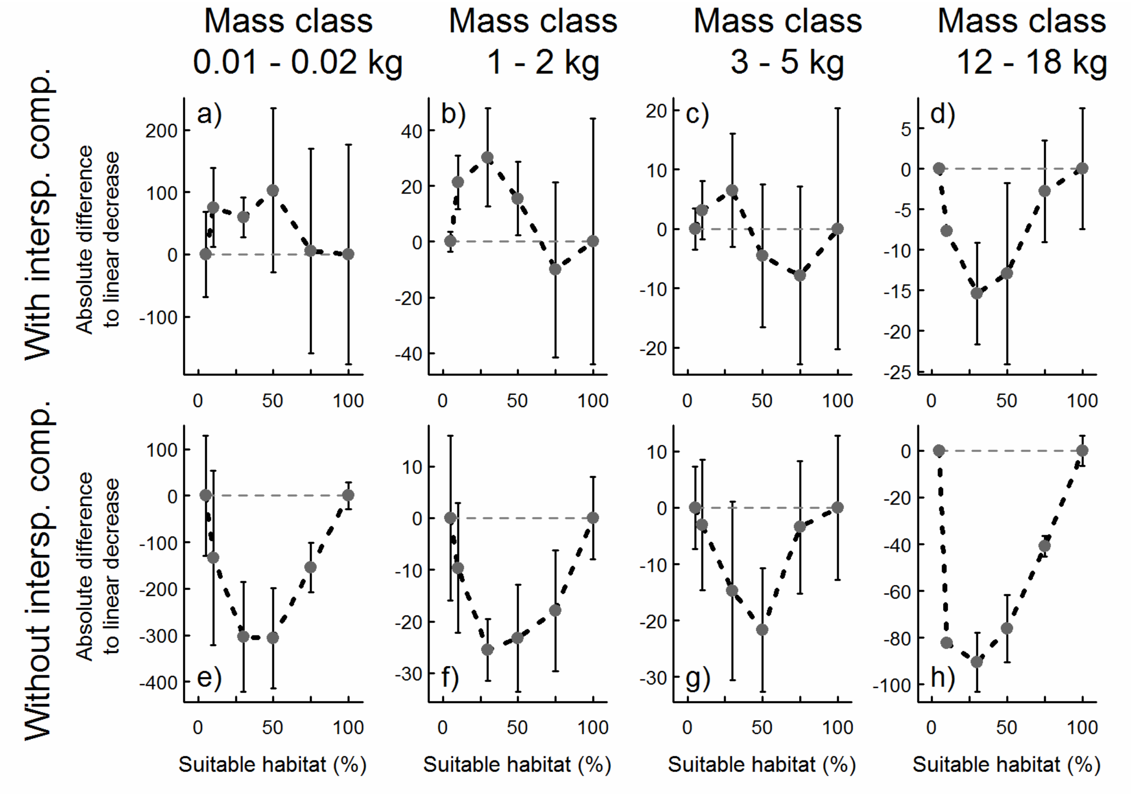

Figure 3.C.1. Effect of habitat loss on the number of birds in smaller mass ranges (representing populations of different species), equivalent to Figs 3.4e-l (for mammals). The horizontal dashed lines connect the population size at highest and lowest habitat area, i.e. they denote a linear decrease of population size with habitat loss. The upper row (a-d) shows the deviation of population size from this linear decrease when the populations are simulated together with the entire community, i.e. with interspecific competition. Below (e-h), this deviation is also shown for simulations of the populations alone, i.e. without competition with individuals outside the respective mass range. Grey symbols show the means, error bars the 95% C.I.s of five landscape replicates with intermediate fragmentation (H = 0.5).

General discussion

In this thesis I have presented results of a new modelling concept that represents a novel way of understanding terrestrial communities by linking processes that determine individual home ranges to the structure of communities. Since the model is mechanistic and spatially explicit the role of different processes for the structure of communities in face of changing habitat structure could be elucidated in unprecedented detail. In Chapter 1 I have introduced the new modelling approach, applied to herbivorous mammals, analysed model behaviour and tested the robustness of model predictions in dependence of parameter settings and resource distribution. In Chapter 2 special focus was given to individual foraging movement, one of the central processes in the model, and how different movement strategies affect community structure in face of habitat loss. Applicability of the model also for birds has been proven in Chapter 3, where the role of space use characteristics and interspecific competition was analysed for mammal and bird communities facing habitat loss and fragmentation.

In the following general discussion I will first summarize and evaluate major results and achievements of this modelling study, structured by major model mechanisms. I will then discuss model limitations before I outline some promising directions for future research and finally subsume the thesis with a general conclusion.

4.1 Animal communities – towards a mechanistic understanding

4.1.1 The link from individual home ranges to community structure

By developing a new allometric modelling approach of individual home range formation in animal communities I have demonstrated that it is possible to link individual physiology and behaviour to community structure. The allometric approach allows for mechanistically simulating home range establishment of individuals not only of a single species, but of animals of a larger range of body masses that interact in heterogeneous landscapes, i.e. an entire community. Besides predicting an explicit distribution of individual home ranges in space, the model explains both, community composition (specifically the individual size distribution ISD, after White et al. 2007) and the allometric relationship between body mass and home range size (Chapter 1, Appendix 3.B), via individual resource use and foraging behaviour in space considering resource competition (mechanisms believed to be most relevant for home range, Harestad and Bunnell 1979, Mitchell and Powell 2004, Said and Servanty 2005). Because patterns in abundance and home range in dependence of body size are complex ecological variables, they have so far been mostly investigated in isolation (e.g. Harestad and Bunnell 1979, Kelt and Van Vuren 2001, Silva and Downing 1995, White et al. 2007, but see Jetz et al. 2004 and Makarieva et al. 2005). Results (Chapter 1) demonstrate that model predictions are largely robust to changes in habitat productivity and habitat fragmentation and that the model can be used to simulate specific communities by only considering explicit body masses of specific species.

The response of model prediction to the values of model parameters reflects the mechanisms underlying home range establishment of individuals (in detail discussed in Chapter 1) and links home range to abundance patterns. The potential resource use of individuals (reflected in the parameter PI, specifically in γ_{PI}, see methods section of Chapter 1) is a key model parameter since it controls home range size, and subsequently also affects community composition (compare Mitchell and Powell 2004, Said and Servanty 2005). In the model presented here daily average potential resource use of individuals in any home range cell (the parameter PI) is assumed to decrease allometrically with body mass – initially without proposing one specific mechanistic explanation. Such negative scaling of potential resource use in the context of individual home range, with an exponent of around-0.25, has been invoked previously and different reasons have been discussed in the literature for decades (from stronger home range overlap of larger animals to fractal resource distributions; see General Introduction and e.g. Kelt and Van Vuren 2001, Haskell et al. 2002, Jetz et al. 2004). In addition to these possible explanations the new movement submodel ‘body mass dependent nomadic movement’ BNF (Chapter 2 and 3) can be interpreted to itself deliver an alternative explanation for the lower potential resource use per day in any single home range cell for larger animals (compared to small animals). The fact that daily movement distance, which is accounted for in this movement model, scales with an exponent that is much smaller than the scaling exponent of home range size, implies that the relative frequency of visiting any specific home range cell decreases with body mass. This agrees with findings of Swihart et al. (1988) who studied the allometry of home range use. Therefore, also the probability of visiting any specific home range location during one day decreases with body mass, which in turn implies that on daily average the potential resource use in that location also decreases. This argumentation also seems reasonable because, besides the literature discussing negative scaling of resource use in the context of home range (e.g. Harestad and Bunnell 1979, Haskell et al. 2002), theory and data indicate a higher potential resource use of larger animals once they are in a specific location (Garland 1983 implicitly assumes resource use per distance moved during a foraging bout in a home range to scale positively with body mass; Carbone et al. 2005 also report positive scaling of local resource use).

Two other crucial model parameters that integrate various, not further specified mechanisms are the exponent of the power law input distribution of body mass and the saturation parameter.

Saturation (either measured directly via the number of occupied home ranges, like in Chapter 1, or determined indirectly via the strongly correlated amount of resources consumed by the community, like in Chapter 2 and 3) describes how far the community is from equilibrium. Environmental variation, predation pressure, community age or assembly time and also disturbance can keep communities from reaching equilibrium (McLeod 1997, Stanford 1995, Mouquet et al. 2003, Makarieva et al. 2005, Starzomski et al. 2008) which can be reflected by the saturation parameter. In contrast, the input distribution reflects the body mass composition of the regional species pool but also integrates processes at larger scales that shape local communities, like dispersal characteristics or colonization potential of the species of the metacommunity (Chapter 1, discussion section, and see Stazomski et al. 2008, Cardillo and Meijaard 2010, Wieher et al. 2011, de Bello in press, for actual research about species pools and environmental 'filters' controlling local communities). Hence, the model describes how regional and local processes act together in shaping the ISD of the local community. The interpretation of the saturation parameter as disturbance agrees with theory of Makarieva et al. (2004, 2005) who state that strongly disturbed systems (i.e. low saturation) are characterized by relatively few small individuals (shallow ISD). In contrast to the argumentation of these authors, who claim home ranges to be mainly determined by genetically encoded characteristics of species and hence, to be insensitive to disturbance, the home ranges in model simulations are controlled by resource use in space (which seems to be a reasonable assumption: Harestad and Bunnell 1979, Mitchell and Powell 2004, Said and Servanty 2005), and are therefore also affected by saturation (disturbance).

4.1.2 The role of movement, space use and competition for community response to landscape modifications

Because the model is spatially explicit and uses realistic grid-based resource landscapes (Hargrove et al. 2002) that can be varied with respect to habitat area and the level of fragmentation of the remaining habitat, it enables one to elucidate the interplay between model mechanisms and landscape properties. Such investigations are urgently needed in order to raise our understanding of how to protect communities in face of the ongoing destruction and subsequent fragmentation of natural habitat, both considered among the greatest contributors to the loss of biodiversity (Harrison and Bruna 1999, Ewers and Didham 2006).

A crucial process for animals in heterogeneous landscapes is foraging movement, because it directly links landscape, and hence the distribution of resources, to individual perception of animals and subsequently determines the use of resources in space. Because movement is a very complex process actual research is dealing with the consequences of different aspects of movement for individuals and populations of single species (Romero et al. 2009, Leblond et al. 2010, Morales et al. 2010, Owen-Smith et al. 2010). So far, however, only large scale movements (dispersal, migration) have been considered in the investigation of (meta-) communities (Büchi et al. 2009, Filotas et al. 2010).

The model introduced here can be used to examine the consequences of small scale (within home range) foraging movements for communities and how these communities cope with habitat loss. Results demonstrate that the efficiency of different movement strategies depends on body mass (Chapter 2). This has in turn profound effects for community structure, as demonstrated for the ISD. While a centre-focussed movement strategy, like central place foraging (CPF), shows a strong body mass limit due to high movement costs in large home ranges (and thus a strong dependence on high resource density close to the home range centre, compare Rhodes et al. 2005), all three foraging movement types tested (CPF, patrolling forager PF and body mass dependent nomadic forager BNF) agree in predicting a shift towards more small animals with increasing habitat loss (steeper ISD exponents, lower 95%-quantile). Such a result corresponds well with empirical studies that indicate a higher vulnerability of larger animals to habitat loss (Ewers and Didham 2006).

Compared to CPF communities, the ISDs of PF and BNF communities are characterized by a higher frequency of large individuals because here ‘foraging on the way’ (during a foraging bout) is allowed. Such foraging reduces the distance that has to be moved for resource acquisition and therefore seems to be essential for larger mammals. Nomadic foraging strategy can be particularly efficient when resources are patchily distributed (Mueller and Fagan 2008). These findings are also reflected in simulation results by larger animals in these communities and in a non-linear response of the ISD to habitat loss.

Detailed insights into the mechanisms controlling the complex non-linear response of communities to landscape modifications can be obtained when different smaller mass windows within the community are regarded separately (Chapter 3). Such mass windows can be interpreted as populations of single species, which allows inference about the response of single populations in the community context. Facing habitat loss, model simulations of populations in interacting mammal and bird communities demonstrate that when large species are not able anymore to establish a home range in a landscape because habitat area is already too low, the next smaller species benefit most, by (relatively) increasing their abundance. Finally, at high levels of habitat loss all resources are shared among the smallest animals. This mechanism of body mass dependent competitive release can explain the delayed response of the ISD exponent compared to the response of the 95%-quantile with habitat loss. Similar phenomena have been reported in carnivororous mammals (‘mesopredator release’, where intermediate sized predators increase in abundance when relieved from predation pressure of large predators, Crooks and Soulé 1999). However, I am not aware of empirical studies reporting this effect of ‘mesocompetitor release’ in herbivores, and its existence in real communities therefore still has to be confirmed.

A comparison between the abundance of populations that are simulated alone and in the community context reveals more novel taxon-specific insights into the role that interspecific competition can play in controlling community response to landscape changes. If populations are simulated alone (i.e. without competition from other mass classes) the effect of fragmentation on mammal and bird populations, is negative for all body sizes, thus adding to the negative effect of habitat loss. In the community context (with interspecific competition), small mammals, however, were found to profit from fragmentation, because they are released from larger competitors, who suffer more strongly from fragmentation (compare Thompson and Fox 1993). Interestingly, such competitive release effects under fragmentation are not observed in birds. Empirical studies indicate that birds can buffer negative effects of landscape modifications because their space use behaviour is more flexible (Ims et al.1993, Redpath 1995, Trzinski et al. 1999, Breitbach et al. 2010). This finding is also reflected in model results, namely that birds respond to fragmentation by adapting the size of their home ranges. While the allometry of simulated home ranges of both taxa shows a similar and rather weak response to habitat loss in scenarios with weak fragmentation, birds significantly increase the size of their home ranges when fragmentation is strong. This higher flexibility with respect to space use in birds compared to mammals can obviously mitigate effects on the ISD of the model community, which is only affected by habitat loss but not by fragmentation (in accordance to findings by Trzinski et al. 1999). This result, in turn explains why competitive release does not play such a prominent role for the response of model bird communities to fragmentation.

Taken together, these results demonstrate that individual physiology and movement behaviour as well as intra- and interspecific competition in space, processes that can explain community composition via individual home range formation, predict complex system response to landscape changes. While major model output is validated with empirical data and principle model behaviour is reasonable considering the home range concept and optimal foraging principles (Chapter 1), some specific predictions on community response to landscape changes, on the role of movement and interspecific competition (Chapters 2 and 3), and of spatial community patterns (Chapter 1) remain to be tested empirically. Because similar modelling approaches have not been used before and collection of appropriate data of entire communities has not yet been accomplished, the model is a valuable tool for generating hypotheses and for motivating further empirical and theoretical research on animal communities. Even if not all of its predictions can be validated directly, the model improves our understanding of the interplay of mechanisms relevant for communities and has implications for the development of effective conservation management (see Chapter 3).

4.2 Model limitations, solutions and prospects for future research

In order to be generic, a model has to simplify complex natural systems. This is particularly the case for a model that aims at mechanistically explaining complex patterns like a body mass distribution of a community in a heterogeneous landscape and its response to changing landscape characteristics. Hence, the primary goal of this thesis was to investigate the interplay of those mechanisms that are believed to be most relevant for community structuring. Clearly, in real systems, further processes can influence community structure, and its response to landscape changes. For example predation, mutualism or parasitism (Wootton 1994, Stachowicz 2001), factors related to population dynamics like lifespan or growth and mortality rates (Wissel et al. 1994), social and behavioural aspects like herding behaviour or territoriality (Ewers and Didham 2006, Banks et al. 2007), fragmentation effects at larger scales like dispersal limitation or isolation (Brown 2007, Flather and Bevers 2002) but also other landscape related effects like matrix or edge effects (Fletcher et al. 2007, Prugh et al. 2008) can shape communities. However, some of these mechanisms that are not explicitly included in the model are implicitly represented by aggregating model parameters (see above). Also the foraging movement types (Chapter 2) are only representing basic movement principles and are implicitly modelled via associated movement costs. Thus, they are simplifications that ignore specific fine scale aspects of movement, for example the response of movement paths to other individuals (compare Moorcroft et al. 2006, Wang and Grimm 2007, Asensio et al. 2011, Giuggioli et al. 2011). Moreover, the fact that in model simulations presented here all individuals consume and compete for one type of resource is a strong assumption. This assumption is, however, a reasonable starting point for testing general principles of community structuring.

The major strength of the model, namely that individuals are only characterized by their body mass, which allows the parameterization by allometric relationships, is also possibly the strongest simplification. However, if a specific community was to be investigated, it would be possible to describe interspecific differences in traits other than body mass (given that sufficient data is available for model parameterization). In Chapter 1, I have demonstrated that in principle simulations with only certain body masses that stand for specific species are possible.

Furthermore, it would be possible to simulate mixed communities, eventually consisting of mammals and birds, in which different species have different, maybe even more specific, foraging strategies. It should also be possible to include species-specific resource distributions (so that not all species compete for the same resource). Here one could investigate the role of the spatial scale of fragmentation by varying the spatial resolution of the specific resource landscape, for example by using smaller grain size for small-bodied individuals. A more sophisticated challenge could be to include predatory species that use the home range distribution of (herbivorous) prey species as their own resource distribution. Preliminary results of simulations with different resource distributions for animals of different mass ranges (data not shown) testing for the effect of different degrees of resource use overlap along a body mass gradient demonstrate interesting effects on the ISD of the community: larger individuals relatively decrease in abundance when niches are separated sharply and profit from higher niche overlap, which reflects their higher competitive ability (compare Oddie 2000, Glazier and Eckert 2002).

To also account for effects of large scale fragmentation (affecting dispersal movement) on communities it seems promising to combine large scale metacommunity models (see Leibold et al. 2004) with small scale individual-based models like the one presented here (compare Hawkes 2009). A first step in this direction could include adjusting the body mass input distribution to changing landscape fragmentation in order to account for landscape effects on the dispersal ability of different species (Etienne and Olff 2004).

A model output that could be investigated in much more detail in the future are the spatially explicit predictions (space use by individuals), and how they depend on movement, resource availability or landscape characteristics (Kertson and Marzluff 2011). It would be interesting to analyse specific aspects of the distribution of individual home ranges in space (e.g. by means of point pattern analysis, Schiffers et al. 2008) or different characteristics of home range overlap in dependence of body mass (Damuth 1981b).

Data that would help to further test model predictions and extend the model include detailed information on resource distributions as well as foraging movement and resource use strategies of several species that interact in a community. Likewise, data on assembly history, individual and community resource use in combination with information on abundance and the spatially explicit distribution of individual home ranges would allow tightening the link between model and real communities. Particularly abundance and home range data of mammal and bird communities in landscapes that differ with respect to habitat area and fragmentation are necessary to assess the relevance of predicted community response to landscape changes for conservation. Additionally such community data, controlled for disturbance, as well as better empirical data on individual resource use in space and time will help to further elaborate on the topics of community saturation and the allometry of potential individual resource use that could not be completely resolved here.

While new and high resolution data on resource distributions can be expected to be obtained using advanced technology in remote sensing (Mueller et al. 2008), the young discipline of movement ecology is about to deliver high resolution movement data of individuals. New advances in tracking technology even enable researchers to simultaneously record physiological and behavioural information of animals (Wilson et al. 2008), which might also help to answer questions on individual resource use Moreover, efforts in order to acquire multi-species movement data have just started. In this context I want to point to the running ‘Automated Radio Telemetry System Initiative’ on Barro Colorado Island which is about to deliver both, movement and physiological data, and the new AgroScapeLabs project (a cooperation of ZALF, Müncheberg and University of Potsdam) in which scientists have just started to obtain first movement data of various species (from hares to wild bores) in an agricultural landscape. Such data in combination with mechanistic modelling approaches (like the one presented here) will help to further increase our understanding of communities facing landscape modifications and should subsequently also help to develop effective conservation measures for animal communities.

4.3 Conclusion

This thesis proves that it is possible to scale from individual physiology and behaviour to the structure of animal communities. This could be achieved by developing a novel allometric approach to mechanistically model the home range establishment of mammals and birds across a wide range of body sizes in heterogeneous landscapes. Thus, the model represents a new way to mechanistically explain community structure and community response to landscape changes via the spatial requirements of individuals that compete for resources. In doing so, the model identifies key parameters for resource use and community structure in space and therefore gives guidance to future empirical research. The mechanistic and spatially explicit nature of the model also allows exploring the effects of habitat loss and fragmentation, and the role that space use, specifically foraging movement, and competition play in controlling these landscape effects on mammals and birds. Simulations predicting individual home ranges and the body mass distribution of the community reveal the strong linkage between these two patterns and the high importance and explanatory power of individual space use for abundance patterns. While general model predictions can be validated with independent data, some specific predictions still have to be considered as hypotheses because the data necessary for their validation do not yet exist. However, results demonstrate the potentially strong effects that competition and foraging strategies have on community response to landscape changes and therefore emphasize the importance to consider movement and space use, as well as species interactions in future efforts to conserve animal communities.

Bibliography

Aars, J., Johannesen, E. and Ims, R. A. (1999) Demographic consequences of movements in subdivided root vole populations. *Oikos*, **85**, 204-216.

Agrawal, A. A. (2004) Resistance and susceptibility of milkweed: competition, root herbivory, and plant genetic variation. *Ecology*, **85**, 2118-2133.

Agrawal, A. A., Ackerly, D. D., Adler, F., Arnold, A. E., Caceres, C., Doak, D. F., Post, E., Hudson, P. J., Maron, J., Mooney, K. A., Power, M., Schemske, D., Stachowicz, J. J., Strauss, S., Turner, M. G. and Werner, E. (2007) Filling key gaps in population and community ecology. *Frontiers in Ecology and the Environment*, **5**, 145-152.

Allen, C. R., Garmestani, A. S., Havlicek, T. D., Marquet, P. A., Peterson, G. D., Restrepo, C., Stow, C. A. and Weeks, B. E. (2006) Patterns in body mass distributions: sifting among alternative hypotheses. *Ecology Letters*, **9**, 630-643.

Andren, H. (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat - a review. *Oikos*, **71**, 355-366.

Asensio, N., Brockelman, W. Y., Malaivijitnond, S. and Reichard, U. H. (2011) Gibbon travel paths are goal oriented. *Animal Cognition*, **14**, 395-405.

Banks, S. C., Piggott, M. P., Stow, A. J. and Taylor, A. C. (2007) Sex and sociality in a disconnected world: a review of the impacts of habitat fragmentation on animal social interactions. *Canadian Journal of Zoology*, **85**, 1065-1079.

Bascompte, J. and Solé, R. V. (1996) Habitat fragmentation and extinction thresholds in spatially explicit models. *Journal of Animal Ecology*, **65**, 465-473.

Basset, A. and Angelis, D. L. (2007) Body size mediated coexistence of consumers competing for resources in space. *Oikos*, **116**, 1363-1377.

Belovsky, G. E. (1987) Extinction models and mammalian persistance. *Viable populations for conservation* (ed. Soulé, M. E.), pp. 35-57. Cambridge University Press, Cambridge.

Benhamou, S. (1996) Space use and foraging movements in the American red squirrel (*Tamiasciurus hudsonicus*). *Behavioural Processes*, **37**, 89-102.

Blackburn, T. M., Brown, V. K., Doube, B. M., Greenwood, J. J. D., Lawton, J. H. and Stork, N. E. (1993) The relationship between abundance and body-size in natural animal assemblages. *Journal of Animal Ecology*, **62**, 519-528.

Blackburn, T. M. and Gaston, K. J. (1994) Animal body-size distributions - patterns, mechanisms and implications. *Trends in Ecology & Evolution*, **9**, 471-474.

Bowers, M. A., Gregario, K., Brame, C. J., Matter, S. F. and Dooley, J. L. (1996a) Use of space and habitats by meadow voles at the home range, patch and landscape scales
6. *Oecologia*, **105**, 107-115.

Bowers, M. A., Matter, S. F., Dooley, J. L., Dauten, J. L. and Simkins, J. A. (1996b) Controlled experiments of habitat fragmentation: a simple computer simulation and a test using small mammals. *Oecologia*, **108**, 182-191.

Bowman, J. (2003) Is dispersal distance of birds proportional to territory size? *Canadian Journal of Zoology*, **81**, 195-202.

Börger, L., Dalziel, B. D. and Fryxell, J. M. (2008) Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecology Letters*, **11**, 637-650.

Breitbach, N., Laube, I., Steffan-Dewenter, I. and Böhning-Gaese, K. (2010) Bird diversity and seed dispersal along a human land-use gradient: high seed removal in structurally simple farmland. *Oecologia*, **162**, 965-976.

Brown, J. H. and Maurer, B. A. (1989) Macroecology - the division of food and space among species on continents. *Science*, **243**, 1145-1150.

Brown, J. H. and Nicoletto, P. F. (1991) Spatial scaling of species composition - body masses of North-American land mammals. *American Naturalist*, **138**, 1478-1512.

Brown, J. H. (1995) *Macroecology*. Chicago University Press, Chicago.

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. and West, G. B. (2004) Toward a metabolic theory of ecology. *Ecology*, **85**, 1771-1789.

Brown, W. P. (2007) Body mass, habitat generality, and avian community composition in forest remnants. *Journal of Biogeography*, **34**, 2168-2181.

Buchmann, C. M., Schurr, F. M., Nathan, R. and Jeltsch, F. (2011a) An allometric model of home range formation explains the structuring of animal communities exploiting heterogeneous resources. *Oikos*, **120**, 106-118.

Buchmann, C. M., Schurr, F. M., Nathan, R. and Jeltsch, F. (2011b) Movement upscaled - the importance of individual foraging movement for community response to habitat loss. *Ecography,* **34**, *001-010.*

Burbidge, A. A. and McKenzie, N. L. (1989) Patterns in the modern decline of Western-Australia vertebrate fauna - causes and conservation implications. *Biological Conservation*, **50**, 143-198.

Burt, W. H. (1943) Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy*, **24**, 346-352.

Büchi, L., Christin, P. A. and Hirzel, A. H. (2009) The influence of environmental spatial structure on the life-history traits and diversity of species in a metacommunity. *Ecological Modelling*, **220**, 2857-2864.

Cagnacci, F., Boitani, L., Powell, R. A. and Boyce, M. S. (2010) Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. *Philosophical Transactions of the Royal Society B - Biological Sciences*, **365**, 2157-2162.

Calder, W. A. III. (1996) *Size, function, and life history*. Dover Publishers Inc., Mineola, New York.

Carbone, C., Cowlishaw, G., Isaac, N. J. B. and Rowcliffe, J. M. (2005) How far do animals go? Determinants of day range in mammals. *American Naturalist*, **165**, 290-297.

Carbone, C., Rowcliffe, J. M., Cowlishaw, G. and Isaac, N. J. B. (2007) The scaling of abundance in consumers and their resources: implications for the energy equivalence rule. *American Naturalist*, **170**, 479-484.

Cardillo, M. and Meijaard, E. (2010) Phylogeny and co-occurrence of mammal species on Southeast Asian islands. *Global Ecology and Biogeography*, **19**, 465-474.

Carfagno, G. L. F. and Weatherhead, P. J. (2008) Energetics and space use: intraspecific and interspecific comparisons of movements and home ranges of two Colubrid snakes. *Journal of Animal Ecology*, **77**, 416-424.

Chatterjee, S., Templin, R. J. and Campbell, K. E. (2007) The aerodynamics of *Argentavis*, the world's largest flying bird from the Miocene of Argentina. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 12398-12403.

Clauset, A. and Erwin, D. H. (2008) The evolution and distribution of species body size. *Science*, **321**, 399-401.

Cotgreave, P. (1993) The relationship between body-size and population abundance in animals. *Trends in Ecology & Evolution*, **8**, 244-248.

Cotgreave, P. and Stockley, P. (1994) Body-size, insectivory and abundance in assemblages of small mammals. *Oikos*, **71**, 89-96.

Crooks, K. R. and Soulé, M. E. (1999) Mesopredator release and avifaunal extinctions in a fragmented system. *Nature*, **400**, 563-566.

Damuth, J. (1981a) Population-density and body size in mammals. *Nature*, **290**, 699-700.

Damuth, J. (1981b) Home range, home range overlap, and species energy use among herbivorous mammals. *Biological Journal of the Linnean Society*, **15**, 185-193.

Damuth, J. (1987) Interspecific allometry of population-density in mammals and other animals - the independence of body-mass and population energy-use. *Biological Journal of the Linnean Society*, **31**, 193-246.

Damuth, J. (2007) A macroevolutionary explanation for energy equivalence in the scaling of body size and population density. *American Naturalist*, **169**, 621-631.

de Bello, F. (in press) The quest for trait convergence and divergence in community assembly: are null-models the magic wand? *Global Ecology and Biogeography.*

Debinski, D. M. and Holt, R. D. (2000) A survey and overview of habitat fragmentation experiments. *Conservation Biology*, **14**, 342-355.

Domis, L. N. D., Mooij, W. M. and Huisman, J. (2007) Climate-induced shifts in an experimental phytoplankton community: a mechanistic approach. *Hydrobiologia*, **584**, 403-413.

Economo, E. P. and Keitt, T. H. (2008) Species diversity in neutral metacommunities: a network approach. *Ecology Letters*, **11**, 52-62.

Ernest, S. K. M. (2005) Body size, energy use, and community structure of small mammals. *Ecology*, **86**, 1407-1413.

Ernest, S. K. M., Brown, J. H., Thibault, K. M., White, E. P. and Goheen, J. R. (2008) Zero sum, the niche, and metacommunities: long-term dynamics of community assembly. *American Naturalist*, **172**, E257-E269.

Etienne, R. S. and Olff, H. (2004) How dispersal limitation shapes species-body size distributions in local communities. *American Naturalist*, **163**, 69-83.

Ewers, R. M. and Didham, R. K. (2006) Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews*, **81**, 117-142.

Fahrig, L. (2002) Effect of habitat fragmentation on the extinction threshold: a synthesis. *Ecological Applications*, **12**, 346-353.

Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology Evolution and Systematics*, **34**, 487-515.

Ficetola, G. F. and Denoel, M. (2009) Ecological thresholds: an assessment of methods to identify abrupt changes in species-habitat relationships. *Ecography*, **32**, 1075-1084.

Fielden, L. J. (1991) Home range and movements of the Namib Desert golden mole, *Eremitalpa granti namibensis* (Chrysochloridae). *Journal of Zoology*, **223**, 675-686.

Filotas, E., Grant, M., Parrott, L. and Rikvold, P. A. (2010) The effect of positive interactions on community structure in a multi-species metacommunity model along an environmental gradient. *Ecological Modelling*, **221**, 885-894.

Flather, C. H. and Bevers, M. (2002) Patchy reaction-diffusion and population abundance: the relative importance of habitat amount and arrangement. *American Naturalist*, **159**, 40-56.

Fletcher, Jr. R. J., Ries, L., Battin, J. and Chalfoun, A. D. (2007) The role of habitat area and edge in fragmented landscapes: definitively distinct or inevitably intertwined? *Canadian Journal of Zoology*, **85**, 1017-1030.

Fryxell, J. M., Hazell, M., Börger, L., Dalziel, B. D., Haydon, D. T., Morales, J. M., McIntosh, T. and Rosatte, R. C. (2008) Multiple movement modes by large herbivores at multiple spatiotemporal scales. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 19114-19119.

Garland, T. (1983) Scaling the ecological cost of transport to body mass in terrestrial mammals. *American Naturalist*, **121**, 571-587.

Gaston, K. J. and Blackburn, T. M. (1996) Conservation implications of geographic range size body size relationships. *Conservation Biology*, **10**, 638-646.

Gautestad, A. O. and Mysterud, I. (2010) Spatial memory, habitat auto-facilitation and the emergence of fractal home range patterns. *Ecological Modelling*, **221**, 2741-2750.

Geffen, E., Gompper, M. E., Gittleman, J. L., Luh, H. K., MacDonald, D. W. and Wayne, R. K. (1996) Size, life-history traits, and social organization in the Canidae: a reevaluation. *American Naturalist*, **147**, 140-160.

Giuggioli, L., Potts, J. R. and Harris, S. (2011) Animal interactions and the emergence of territoriality. *Plos Computational Biology*, **7**, e1002008.

Glazier, D. S. and Eckert, S. E. (2002) Competitive ability, body size and geographical range size in small mammals. *Journal of Biogeography*, **29**, 81-92.

Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W. M., Railsback, S. F., Thulke, H. H., Weiner, J., Wiegand, T. and DeAngelis, D. L. (2005) Pattern-oriented modeling of agent-based complex systems: lessons from ecology. *Science*, **310**, 987-991.

Grimm, V., Berger, U., DeAngelis, D. L., Polhill, J. G., Giske, J. and Railsback, S. F. (2010) The ODD protocol: a review and first update. *Ecological Modelling*, **221**, 2760-2768.

Harestad, A. S. and Bunnell, F. L. (1979) Home range and body weight - reevaluation. *Ecology*, **60**, 389-402.

Hargrove, W. W., Hoffman, F. M. and Schwartz, P. M. (2002) A fractal landscape realizer for generating synthetic maps. *Conservation Ecology*, **6**, article 2.

Harrison, S. and Bruna, E. (1999) Habitat fragmentation and large-scale conservation: what do we know for sure? *Ecography*, **22**, 225-232.

Haskell, J. P., Ritchie, M. E. and Olff, H. (2002) Fractal geometry predicts varying body size scaling relationships for mammal and bird home ranges. *Nature*, **418**, 527-530.

Hawkes, C. (2009) Linking movement behaviour, dispersal and population processes: is individual variation a key? *Journal of Animal Ecology*, **78**, 894-906.

Hendriks, A. J., Willers, B. J. C., Lenders, H. J. R. and Leuven, R. S. E. W. (2009) Towards a coherent allometric framework for individual home ranges, key population patches and geographic ranges. *Ecography*, **32**, 929-942.

Henle, K., Davies, K. F., Kleyer, M., Margules, C. and Settele, J. (2004) Predictors of species sensitivity to fragmentation. *Biodiversity and Conservation*, **13**, 207-251.

Hibert, F., Calenge, C., Fritz, H., Maillard, D., Bouche, P., Ipavec, A., Convers, A., Ombredane, D. and de Visscher, M. N. (2010) Spatial avoidance of invading pastoral cattle by wild ungulates: insights from using point process statistics. *Biodiversity and Conservation*, **19**, 2003-2024.

Hinsley, S. A. (2000) The costs of multiple patch use by birds. *Landscape Ecology*, **15**, 765-775.

Holden, C. (2006) Inching toward movement ecology. *Science*, **313**, 779-782.

Holling, C. S. (1992) Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecological Monographs*, **62**, 447-502.

Houle, M., Fortin, D., Dussault, C., Courtois, R. and Ouellet, J. P. (2010) Cumulative effects of forestry on habitat use by gray wolf (*Canis lupus*) in the boreal forest. *Landscape Ecology*, **25**, 419-433.

Hubbell, S. P. (2001) *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, New Jersey.

Hubbell, S. P. (2006) Neutral theory and the evolution of ecological equivalence. *Ecology*, **87**, 1387-1398.

Ims, R. A., Rolstad, J. and Wegge, P. (1993) Predicting space use responses to habitat fragmentation: can voles *Microtus oeconomus* serve as an experimental model system (EMS) for capercaillie grouse *Tetrao urogallus* in boreal forest. *Biological Conservation*, **63**, 261-268.

Jeltsch, F., Moloney, K. A., Schurr, F. M., Kochy, M. and Schwager, M. (2008) The state of plant population modelling in light of environmental change. *Perspectives in Plant Ecology Evolution and Systematics*, **9**, 171-189.

Jeltsch, F., Moloney, K. A., Schwager, M., Körner, K. and Blaum, N. (2011) Consequences of correlations between habitat modifications and negative impact of climate change for regional species survival. *Agriculture, Ecosystems and Environment*, **145**, 49-58.

Jetz, W., Carbone, C. and Fulford, J. (2004) The scaling of animal space use. *Science*, **306**, 266-268.

Kadmon, R. and Allouche, O. (2007) Integrating the effects of area, isolation, and habitat heterogeneity on species diversity: a unification of island biogeography and niche theory. *American Naturalist*, **170**, 443-454.

Kareiva, P., Mullen, A. and Southwood, R. (1990) Population dynamics in spatially complex environments: theory and data. *Philosophical Transactions of the Royal Society B - Biological Sciences*, **330**, 175-190.

Kelt, D. A. and Van Vuren, D. H. (2001) The ecology and macroecology of mammalian home range area. *American Naturalist*, **157**, 637-645.

Kertson, B. N. and Marzluff, J. M. (2011) Improving studies of resource selection by understanding resource use. *Environmental Conservation*, **38**, 18-27.

Koenker, R. (2009) Quantreg: quantile regression. R package version 4.30.

Körner, K. and Jeltsch, F. (2008) Detecting general plant functional type responses in fragmented landscapes using spatially-explicit simulations. *Ecological Modelling*, **210**, 287-300.

Körner, K., Treydte, A., Burkart, M. and Jeltsch, F. (2010) Simulating direct and indirect effects of climatic changes on rare perennial plant species in fragmented landscapes. *Journal of Vegetation Science*, **21**, 843-856.

Larsen, T. H., Lopera, A. and Forsyth, A. (2008) Understanding trait-dependent community disassembly: dung beetles, density functions, and forest fragmentation. *Conservation Biology*, **22**, 1288-1298.

Lawton, J. H. (1990) Species richness and population-dynamics of animal assemblages - patterns in body size - abundance space. *Philosophical Transactions of the Royal Society B - Biological Sciences*, **330**, 283-291.

Leblond, M., Dussault, C. and Ouellet, J. P. (2010) What drives fine-scale movements of large herbivores? A case study using moose. *Ecography*, **33**, 1102-1112.

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt, R. D., Shurin, J. B., Law, R., Tilman, D., Loreau, M. and Gonzalez, A. (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters*, **7**, 601-613.

Lindell, C. A., Riffell, S. K., Kaiser, S. A., Battin, A. L., Smith, M. L. and Sisk, T. D. (2007) Edge responses of tropical and temperate birds. *Wilson Journal of Ornithology*, **119**, 205-220.

Lindstedt, S. L., Miller, B. J. and Buskirk, S. W. (1986) Home range, time, and body size in mammals. *Ecology*, **67**, 413-418.

Loehle, C. (2006) Species abundance distributions result from body size-energetics relationships. *Ecology*, **87**, 2221-2226.

MacArthur, R. H. (1957) On the relative abundance of bird species. *Proceedings of the National Academy of Sciences of the United States of America*, **43**, 293-295.

MacArthur, R. H. (1960) On the relative abundance of species. *American Naturalist*, **94**, 25-36.

Makarieva, A. M., Gorshkov, V. G. and Li, B. L. (2004) Body size, energy consumption and allometric scaling: a new dimension in the diversity-stability debate. *Ecological Complexity*, **1**, 139-175.

Makarieva, A. M., Gorshkov, V. G. and Li, B.-L. (2005) Why do population density and inverse home range scale differently with body size? Implications for ecosystem stability. *Ecological Complexity*, **2**, 259-271.

May, F., Grimm, V. and Jeltsch, F. (2009) Reversed effects of grazing on plant diversity: the role of below-ground competition and size symmetry. *Oikos*, **118**, 1830-1843.

May, R. M. (1975) Patterns of species abundance and diversity. *Ecology and evolution of communities* (eds. Cody, M. I. and Diamond, J. M.), pp. 81-120. Harvard University Press, Cambridge, Massachusetts.

McCann, K. I. and Benn, G. I. (2006) Land use patterns within Wattled Crane (*Bugeranus carunculatus*) home ranges in an agricultural landscape in KwaZulu-Natal, South Africa. *Ostrich*, **77**, 186-194.

McGill, B. J., Enquist, B. J., Weiher, E. and Westoby, M. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, **21**, 178-185.

McLaughlin, R. L. (1989) Search modes of birds and lizards - evidence for alternative movement patterns. *American Naturalist* , **133**, 654-670.

McLeod, S. R. (1997) Is the concept of carrying capacity useful in variable environments? *Oikos*, **79**, 529-542.

Mitchell, M. S. and Powell, R. A. (2004) A mechanistic home range model for optimal use of spatially distributed resources. *Ecological Modelling*, **177**, 209-232.

Moorcroft, P. R., Lewis, M. A. and Crabtree, R. L. (2006) Mechanistic home range models capture spatial patterns and dynamics of coyote territories in Yellowstone. *Proceedings of the Royal Society B - Biological Sciences*, **273**, 1651-1659.

Morales, J. M., Moorcroft, P. R., Matthiopoulos, J., Frair, J. L., Kie, J. G., Powell, R. A., Merrill, E. H. and Haydon, D. T. (2010) Building the bridge between animal movement and population dynamics. *Philosophical Transactions of the Royal Society B - Biological Sciences*, **365**, 2289-2301.

Motomura, I. (1932) On the statistical treatment of communities. *Zoological Magazine, Tokyo*, **44**, 379-383.

Mouquet, N., Munguia, P., Kneitel, J. M. and Miller, T. E. (2003) Community assembly time and the relationship between local and regional species richness. *Oikos*, **103**, 618-626.

Mueller, T. and Fagan, W. F. (2008) Search and navigation in dynamic environments - from individual behaviors to population distributions. *Oikos*, **117**, 654-664.

Mueller, T., Olson, K. A., Fuller, T. K., Schaller, G. B., Murray, M. G. and Leimgruber, P. (2008) In search of forage: predicting dynamic habitats of Mongolian gazelles using satellite-based estimates of vegetation productivity. *Journal of Applied Ecology*, **45**, 649-658.

Nagy, K. A. (2001) Food requirements of wild animals: predictive equations for free-living mammals, reptiles, and birds. *Nutrition Abstracts and Reviews, Series B*, **71**, 21R-31R.

Nathan, R., Getz, W. M., Revilla, E., Holoyoak, M., Kadmon, R., Saltz, D. and Smouse, P. E. (2008) A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 19052-19059.

Nee, S. and May, R. M. (1992) Dynamics of metapopulations - habitat destruction and competitive coexistence. *Journal of Animal Ecology*, **61**, 37-40.

Nonaka, E. and Holme, P. (2007) Agent-based model approach to optimal foraging in heterogeneous landscapes: effects of patch clumpiness. *Ecography*, **30**, 777-788.

Norris, D., Michalski, F. and Peres, C. A. (2010) Habitat patch size modulates terrestrial mammal activity patterns in Amazonian forest fragments. *Journal of Mammalogy*, **91**, 551-560.

Oddie, K. R. (2000) Size matters: competition between male and female great tit offspring. *Journal of Animal Ecology*, **69**, 903-912.

Orland, M. C. and Kelt, D. A. (2007) Responses of a heteromyid rodent community to large- and small-scale resource pulses: diversity, abundance, and home-range dynamics. *Journal of Mammalogy*, **88**, 1280-1287.

Ottaviani, D., Cairns, S. C. and Oliverio, M. (2006) Body mass as a predictive variable of home-range size among Italian mammals and birds. *Journal of Zoology*, **269**, 317-330.

Owen-Smith, N., Fryxell, J. M. and Merrill, E. H. (2010) Foraging theory upscaled: the behavioural ecology of herbivore movement. *Philosophical Transactions of the Royal Society B - Biological Sciences*, **365**, 2267-2278.

Pagel, M. D. and Harvey, P. H. (1988) Recent developments in the analysis of comparative data. *Quarterly Review of Biology*, **63**, 413-440.

Patterson, T. A., Thomas, L., Wilcox, C., Ovaskainen, O. and Matthiopoulos, J. (2008) State-space models of individual animal movement. *Trends in Ecology & Evolution*, **23**, 87-94.

Peters, R. H. (1983) *The ecological implications of body size*. Cambridge University Press, Cambridge.

Pita, R., Mira, A. and Beja, P. (2010) Spatial segregation of two vole species (*Arvicola sapidus* and *Microtus cabrerae*) within habitat patches in a highly fragmented farmland landscape. *European Journal of Wildlife Research*, **56**, 651-662.

Preston, F. W. (1948) The commonness, and rarity, of species. *Ecology*, **29**, 254-283.

Prugh, L. R., Hodges, K. E., Sinclair, A. R. E. and Brashares, J. S. (2008) Effect of habitat area and isolation on fragmented animal populations. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 20770-20775.

R Development Core Team. (2008) *R: a language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0.

Redpath, S. M. (1995) Habitat fragmentation and the individual: tawny owls *Strix Aluco* in woodland patches. *Journal of Animal Ecology*, **64**, 652-661.

Reuman, D. C., Mulder, C., Raffaelli, D. and Cohen, J. E. (2008) Three allometric relations of population density to body mass: theoretical integration and empirical tests in 149 food webs. *Ecology Letters*, **11**, 1216-1228.

Reuter, H. (2005) Community processes as emergent properties: modelling multilevel interaction in small mammals communities. *Ecological Modelling*, **186**, 427-446.

Rhodes, J. R., McAlpine, C. A., Lunney, D. and Possingham, H. P. (2005) A spatially explicit habitat selection model incorporating home range behavior. *Ecology*, **86**, 1199-1205.

Ritchie, M. E. (1998) Scale-dependent foraging and patch choice in fractal environments. *Evolutionary Ecology*, **12**, 309-330.

Ritchie, M. E. and Olff, H. (1999) Spatial scaling laws yield a synthetic theory of biodiversity. *Nature*, **400**, 557-560.

Rohwer, S., Ricklefs, R. E., Rohwer, V. G. and Copple, M. M. (2009) Allometry of the duration of flight feather molt in birds. *PLOS Biology*, **7**, e1000132.

Romero, S., Campbell, J. F., Nechols, J. R. and With, K. A. (2009) Movement behavior in response to landscape structure: the role of functional grain. *Landscape Ecology*, **24**, 39-51.

Russell, R. E., Swihart, R. K. and Feng, Z. L. (2003) Population consequences of movement decisions in a patchy landscape. *Oikos*, **103**, 142-152.

Said, S. and Servanty, S. (2005) The influence of landscape structure on female roe deer home-range size. *Landscape Ecology*, **20**, 1003-1012.

Said, S., Gaillard, J. M., Widmer, O., Debias, F., Bourgoin, G., Delorme, D. and Roux, C. (2009) What shapes intra-specific variation in home range size? A case study of female roe deer. *Oikos*, **118**, 1299-1306.

Saupe, D. (1988) Algorithms for random fractals. *The Science of Fractal Images* (ed. Petigen, H. O. and Saupe, D.), pp. 71-113. Springer, New York.

Scharf, I., Nulman, E., Ovadia, O. and Bouskila, A. (2006) Efficiency evaluation of two competing foraging modes under different conditions. *American Naturalist*, **168**, 350-357.

Schick, R. S., Loarie, S. R., Colchero, F., Best, B. D., Boustany, A., Conde, D. A., Halpin, P. N., Joppa, L. N., McClellan, C. M. and Clark, J. S. (2008) Understanding movement data and movement processes: current and emerging directions. *Ecology Letters*, **11**, 1338-1350.

Schiffers, K., Schurr, F. M., Tielbörger, K., Urbach, C., Moloney, K. and Jeltsch, F. (2008) Dealing with virtual aggregation - a new index for analysing heterogeneous point patterns. *Ecography*, **31**, 545-555.

Selonen, V., Hanski, I. K. and Stevens, P. C. (2001) Space use of the Siberian flying squirrel *Pteromys volans* in fragmented forest landscapes. *Ecography*, **24**, 588-600.

Shipley, L. A. (2007) The influence of bite size on foraging at larger spatial and temporal scales by mammalian herbivores. *Oikos*, **116**, 1964-1974.

Silva, M. and Downing, J. A. (1995) The allometric scaling of density and body-mass - a nonlinear relationship for terrestrial mammals. *American Naturalist*, **145**, 704-727.

Skorka, P., Lenda, M., Martyka, R. and Tworek, S. (2009) The use of metapopulation and optimal foraging theories to predict movement and foraging decisions of mobile animals in heterogeneous landscapes. *Landscape Ecology*, **24**, 599-609.

Smith, A. C., Fahrig, L. and Francis, C. M. (2011) Landscape size affects the relative importance of habitat amount, habitat fragmentation, and matrix quality on forest birds. *Ecography*, **34**, 103-113.

Stachowicz, J. J. (2001) Mutualism, facilitation, and the structure of ecological communities. *Bioscience*, **51**, 235-246.

Stanford, C. B. (1995) The influence of chimpanzee predation on group size and anti-predator behavior in red colobus monkeys. *Animal Behaviour*, **49**, 577-587.

Starzomski, B. M., Parker, R. L. and Srivastava, D. S. (2008) On the relationship between regional and local species richness: a test of saturation theory. *Ecology*, **89**, 1921-1930.

Sutherland, G. D., Harestad, A. S., Price, K. and Lertzman, K. P. (2000) Scaling of natal dispersal distances in terrestrial birds and mammals. *Conservation Ecology*, **4**, article 16.

Swift, T. L. and Hannon, S. J. (2010) Critical thresholds associated with habitat loss: a review of the concepts, evidence, and applications. *Biological Reviews*, **85**, 35-53.

Swihart, R. K., Slade, N. A. and Bergstrom, B. J. (1988) Relating body size to the rate of home range use in mammals. *Ecology*, **69**, 393-399.

Thompson, P. and Fox, B. J. (1993) Asymmetric competition in Australian heathland rodents - a reciprocal removal experiment demonstrating the influence of size-class structure. *Oikos*, **67**, 264-278.

Tristiani, H., Murakami, O. and Watanabe, H. (2003) Ranging and nesting behavior of the ricefield rat *Rattus argentiventer* (Rodentia: Muridae) in West Java, Indonesia. *Journal of Mammalogy*, **84**, 1228-1236.

Trzcinski, M. K., Fahrig, L. and Merriam, G. (1999) Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. *Ecological Applications*, **9**, 586-593.

Van Moorter, M., Visscher, D., Benhamou, S., Börger, L., Boyce, M. S. and Gaillard, J.-M. (2009) Memory keeps you at home: a mechanistic model for home range emergence. *Oikos*, **118**, 641-652.

Vucetich, J. A., Peterson, R. O. and Waite, T. A. (1997) Effects of social structure and prey dynamics on extinction risk in gray wolves. *Conservation Biology*, **11**, 957-965.

Wang, M. and Grimm, V. (2007) Home range dynamics and population regulation: an individual-based model of the common shrew *Sorex ayaneus*. *Ecological Modelling*, **205**, 397-409.

Weiher, E., Freund, D., Bunton, T., Stefanski, A., Lee, T. and Bentivenga, S. (2011) Advances, challenges and a developing synthesis of ecological community assembly theory. *Philosophical Transactions of the Royal Society B - Biological Sciences*, **366**, 2403-2413.

West, G. B., Woodruff, W. H. and Brown, J. H. (2002) Allometric scaling of metabolic rate from molecules and mitochondria to cells and mammals. *Proceedings of the National Academy of Sciences of the United States of America*, **99**, 2473-2478.

White, E. P., Ernest, S. K. M., Kerkhoff, A. J. and Enquist, B. J. (2007) Relationships between body size and abundance in ecology. *Trends in Ecology & Evolution*, **22**, 323-330.

Whittaker, R. H. (1975) *Communities and Ecosystems*. MacMillan, London.

Wiegand, K., Jeltsch, F. and Ward, D. (2000) Do spatial effects play a role in the spatial distribution of desert-dwelling *Acacia raddiana*? *Journal of Vegetation Science*, **11**, 473-484.

Wiegand, T., Knauer, F., Kaczensky, P. and Naves, J. (2004) Expansion of brown bears (*Ursus arctos*) into the Eastern Alps: a spatially explicit population model. *Biodiversity and Conservation*, **13**, 79-114.

Wilcox, B. A. and Murphy, D. D. (1985) Conservation strategy - the effects of fragmentation on extinction. *American Naturalist*, **125**, 879-887.

Wilmers, C. C., Post, E. and Hastings, A. (2007) The anatomy of predator-prey dynamics in a changing climate. *Journal of Animal Ecology*, **76**, 1037-1044.

Wilson, R. P., Shepard, E. L. C. and Liebsch, N. (2008) Prying into the intimate details of animal lives: use of a daily diary on animals. *Endangered Species Research*, **4**, 123-137.

Wissel, C., Stephan, T. and Zaschke, S. (1994) Modelling extinction and survival of small populations. *Minimum viable populations* (ed. Remmert, H.), pp. 67-103. Springer, Heidelberg.

With, K. A. and Crist, T. O. (1995) Critical thresholds in species responses to landscape structure. *Ecology*, **76**, 2446-2459.

With, K. A. (1997) The application of neutral landscape models in conservation biology. *Conservation Biology*, **11**, 1069-1080.

Wootton, J. T. (1994) The nature and consequences of indirect effects in ecological communities. *Annual Review of Ecology and Systematics*, **25**, 443-466.

Yaacobi, G., Ziv, Y. and Rosenzweig, M. L. (2007) Effects of interactive scale-dependent variables on beetle diversity patterns in a semi-arid agricultural landscape. *Landscape Ecology*, **22**, 687-703.

Zusammenfassung

Seit Jahrzehnten ist die Beantwortung der Frage nach den Mechanismen, welche die Zusammensetzung, aber auch die räumliche Struktur von Artengemeinschaften bestimmen, eine der großen Herausforderungen in der Ökologie. Ein derartiges mechanistisches Verständnis ist Vorraussetzung, um vorhersagen zu können wie Tiergemeinschaften von Umweltveränderungen, wie beispielsweise Habitatverlust und Habitatfragmentierung, beeinflusst werden. Der größte Teil existierender empirischer und theoretischer Studien beschäftigt sich allerdings weitestgehend mit Einzelarten. Die wenigen theoretischen Modellstudien auf der Ebene von Tiergemeinschaften sind entweder nicht räumlich explizit, wodurch komplexe Landschaftseffekte nicht betrachtet werden können, oder berücksichtigen nur großräumige Landschaftseffekte welche sich auf die Ausbreitungsbewegungen von Tieren auswirken. Jedoch entscheiden räumliche Prozesse auf kleinerer Skala wie Tiere mit veränderten Ressourcenverteilungen im Raum zu Recht kommen, und dürfen daher nicht ignoriert werden. Die Etablierung von individuellen Aktionsräumen (engl. ‘home ranges’) ist in diesem Zusammenhang von besonderer Bedeutung ist, da sie sowohl die Physiologie und das Verhalten von Individuen (wie Bewegungsstrategien zur Nahrungssuche) als auch inner- sowie zwischenartliche Ressourcenkonkurrenz im Raum einschließt.

In dieser Arbeit wird ein neuartiger individuen-basierter Modellierungsansatz vorgestellt, welcher erstmals eine Tiergemeinschaft artübergreifend auf der Basis der Etablierung von individuellen Aktionsräumen räumlich explizit simuliert. Dabei werden etablierte (empirisch ermittelte) so genannten allometrischen Beziehungen verwendet, welche den mathematischen Zusammenhang zwischen der Körpermasse eines Tieres und vor allem physiologischen aber auch ökologischen Eigenschaften beschreiben. Dadurch gelingt es, Aktionsraum-Etablierung für Säugetiere und Vögel einer ganzen Gemeinschaft (d.h. verschiedenster Körpermassen) zu modellieren

Im ersten Kapitel wird das Modell, parametrisiert für Säugetiere, vorgestellt, das Modellverhalten in Abhängigkeit von Parametern beleuchtet, sowie die Robustheit der Modellvorhersagen untersucht. Neben Vorhersagen über die räumliche Verteilung aller Aktionsräume liefert das Modell realistische Ergebnisse bezüglich der allometrischen Beziehung zwischen Körpermasse und Aktionsraumgröße sowie der Körpermassenverteilung (Größenspektrum) der Tiergemeinschaft. Diese Ergebnisse verdeutlichen die wichtige Rolle von räumlicher Ressourcennutzung und Aktionsräumen für die Zusammensetzung von Tiergemeinschaften.

Im zweiten Kapitel werden drei grundlegend verschiedene Bewegungsstrategien zur Nahrungssuche (‘zentrums-fokussiert’, ‘patroullierend’, und ‘nomadisch’) in das Modell integriert und untersucht. Die Effizienz der einzelnen Strategien ist von der jeweiligen Körpermasse abhängig, was wiederum einen Effekt darauf hat, wie sich Habitatverlust auf eine Tiergemeinschaft auswirkt. Während ‘zentrums-fokussierte’ Nahrungssuche nur für kleine Säugetiere effizient ist, ist gerade der nomadische Bewegungstyp für große Tiere vorteilhaft, was sich in einer verzögerten Reaktion der Körpermassenverteilung dieser Tiere bei fortschreitendem Habitatverlust widerspiegelt.

Derart komplexes, nichtlineares Modellverhalten bezüglich der Körpemassenverteilungen von Säugetier- und Vogelgemeinschaften bei Habitatverlust und Habitatfragmentierung wird im dritten Kapitel beleuchtet und erklärt: Dadurch dass sich größere Säuger und Vögel bei fortschreitendem Habitatverlust nicht mehr etablieren können, profitieren kleinere Individuen von der Verringerung dieses Konkurrenzdrucks. Durch diesen Effekt können kleine Säuger sogar von Habitatfragmentierung, welche in der Regel einen großen negativen Effekt auf die Körpermassenverteilung von Säugetieren hat, profitieren. Auf die Körpermassenverteilung von Vogelgemeinschaften hat Fragmentierung einen wesentlich geringeren Einfluss, da diese die Größe ihrer Aktionsräume den Bedingungen anpassen, und somit Fragmentierungseffekte großteils kompensieren können.

Indem es die Strukturierung von Tiergemeinschaften auf Basis von individuellen Eigenschaften (Physiologie und Verhalten) beschreibt, stellt das hier präsentierte Modell einen neue Art und Weise dar, Tiergemeinschaften und deren Reaktion auf Landschaftsveränderungen zu erklären. Die Ergebnisse veranschaulichen die potentiell große Bedeutung von kleinskaligen Bewegungsstrategien, Aktionsräumen und zwischenartlicher Konkurrenz, und weisen damit auf die Relevanz dieser Prozesse für die Entwicklung effizienter Schutzmaßnahmen für Tiergemeinschaften hin.

Danksagung

Ich möchte mich bei einigen Menschen sehr herzlich bedanken, die mich im Laufe meiner Promotion unterstützt haben.

Zu allererst natürlich bei meinen beiden Haupt-Betreuern Florian Jeltsch und Frank Schurr. Florian vielen Dank für das Vertrauen in mich, von Anfang an, welches mich enorm motiviert und angespornt hat, für die vielen Freiräume die Du mir gelassen hast, und für die vielen guten lösungsorientierten Diskussionen. Aber auch vor allem vielen Dank für Deine besondere Unterstützung wenn dann mal wirklich ‘Not am Mann’ war.

Frank, auch Dir vielen Dank für die meist extrem output-reichen Gespräche, die kritischen Fragen (meist inklusive der richtigen Antworten), und vor allem die Unterstützung bzgl. statistischer und mathematischer Details. Und ohne Dich würde ich wahrscheinlich immer noch mit irgendwelchen selbst gebastelten Fitting-Routinen rum-doktern.

Des Weiteren möchte ich Ran Nathan danken, der ursprünglich die Idee zu dieser Promotion entwickelt hatte, und auch gerade am Anfang meiner Promotion stark in die thematischen Diskussionen involviert war. Mit seiner Expertise war er eine große Hilfe, und hat es dadurch geschafft meinem Glauben an diese Arbeit zu bestärken.

Jana, Niels und Eva, vielen Dank auch Euch für die Gespräche mit Euch, speziell für Eure Hilfe meine doch sehr theoretische Arbeit mit der wirklichen zoologischen Welt ein bisschen mehr zusammenzubringen. Volker Grimm möchte ich dafür danken, dass ich durch Dich so spielerisch C++ lernen durfte, und dass Du auch immer da warst wenn es nötig war (ob bzgl. ODD oder bei Fragen im Publikations-Prozess).

Als nächstes möchte ich mich noch bei vielen (auch Ex-) Mitgliedern der Arbeitsgruppe bedanken; ich habe die Zeit in dieser AG, von guten thematischen Gesprächen bis zu den Kaffeepausen und aber vor allem den ziemlich vielen anderen Aktivitäten, meist sehr genossen. Da ich sicher jemanden vergesse lasse ich hier das mit den Namen bleiben. Ihr wisst dass ich Euch meine.

Britta, danke für Deine Kommentare zu Teilen dieser Arbeit, und überhaupt fürs oft-dasein! Tobi, danke fürs extra-ans-PIK fahren! Danke an viele andere sehr gute Freunde in Potsdam, die mich doch hin und wieder (vielleicht auch öfter) aufbauen und motivieren mussten – das aber gut hingekriegt haben.

Zu allerletzt Danke an meine Familie, dass Ihr immer hinter mir gestanden habt, und mich bis hierhin unterstützt habt!

Declaration

This thesis comprises three scientific studies that investigate the role of individual home range formation, specifically foraging movement and competition for the structuring of terrestrial animal communities. The model (and its extensions) that was used for these investigations was implemented by myself, I conducted all simulations as well analyses in all three studies and wrote all contents of this thesis by myself, supported by comments and advice from supervisors and co-authors. Where data by others was used, it is indicated in the text.

The three chapters are written as independent articles in cooperation with co-authors, and therefore entail a certain amount of repetition. Chapters 1 and 2 are published, and therefore contain referees' and editors' comments and suggestions.