



An allometric model of home range formation explains the structuring of animal communities exploiting heterogeneous resources

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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.

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 1981a, 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: (1) it has to describe both intra- and interspecific competition for resources affecting home range selection, and (2) 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 (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 Basset 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 (1) home range size and (2) abundance, i.e. can it explain two complex community patterns at once, (3) how robust are the predicted relationships to changes in resource availability and landscape heterogeneity, and (4) what lessons can be learned about the role of spatially-explicit, interspecific resource competition in shaping animal communities.

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) 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.

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

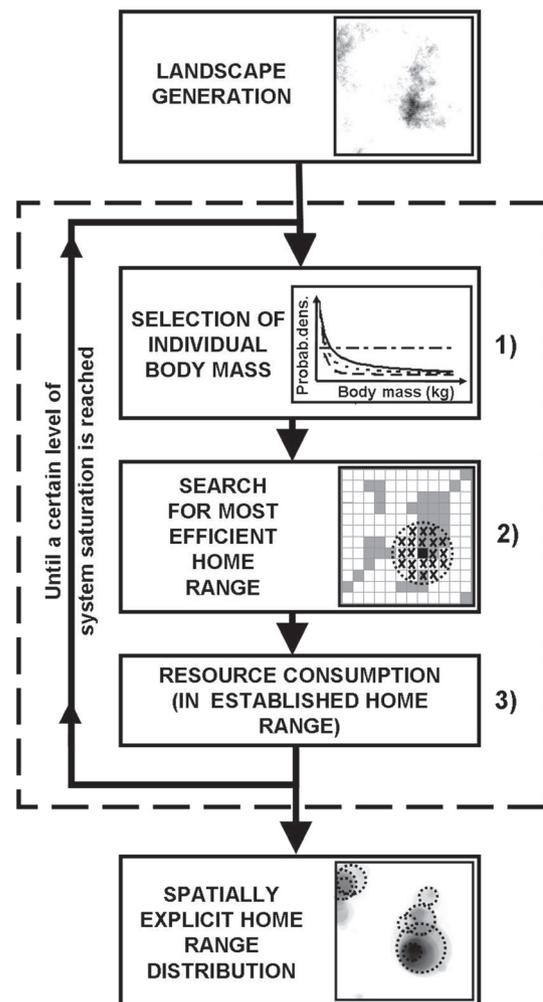


Figure 1. Flow chart showing the main elements of the allometric model for home range formation in animal communities.

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.

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 ; $\sigma^2 = 30$ 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 km²). 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 km²).

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 \times m⁻² \times year⁻¹ (equivalent to an average of 6.85×10^{-2} kg dry biomass \times grid cell⁻¹ \times 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).

Selection of individual body mass

Individual animals are characterized by their body mass (M), which can vary between 0.005 kg 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

$$p(M) = \kappa \times M^\eta \quad (1)$$

with p representing the probability density of a certain body mass M . The normalization constant κ was chosen so that Eq. 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.

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

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

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.

$$IG_i = R_i \times PC \times PI \text{ (kg dry biomass)} \quad (3)$$

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 1981a, 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 :

$$PI = \gamma_{PI} \times \frac{M^{-0.25}}{0.001 \text{kg}^{-0.25}} \quad (M \text{ in kg}) \quad (4)$$

where the coefficient γ_{PI} , determining the general magnitude of PI, is a systematically tested model parameter. The denominator ($0.001 \text{kg}^{-0.25}$) 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 by 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

$$IGN_i = IG_i - LC_i \quad (\text{kg dry biomass}) \quad (5)$$

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):

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

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

$$LC_i = \frac{d_i \times MC}{f} \quad (\text{kg dry biomass}) \quad (7)$$

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 $1.00 \times 10^7 \text{ J} \times \text{kg dry biomass intake}^{-1}$ (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

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

$$HR_{\text{max-herb}} = 47.86 \times M^{1.18} \quad (\text{ha}, M \text{ in kg}) \quad (9)$$

given in Kelt and Van Vuren (2001) as the maximum of a constraint space of home range area for herbivores (Eq. 8) and omnivores (Eq. 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. 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.

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).

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 γ_{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). Supplementary material Appendix 1 describes in detail how the saturation approach (using SATan) is implemented.

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), 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) (Supplementary material Appendix 1). 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 1981b).

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 analyzed 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 1981b, 2007, Brown et al. 2004, Makarieva et al. 2005). 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 Eq. 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 Supplementary material Appendix 2, Tables A2.1, A2.2 and A2.3). The values of η predicted by our model were similarly obtained by maximum likelihood fitting of Eq. 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 (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.

Results

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. 2). While home range centres of larger animals are located in the middle of large resource patches, smaller individuals tend to establish home

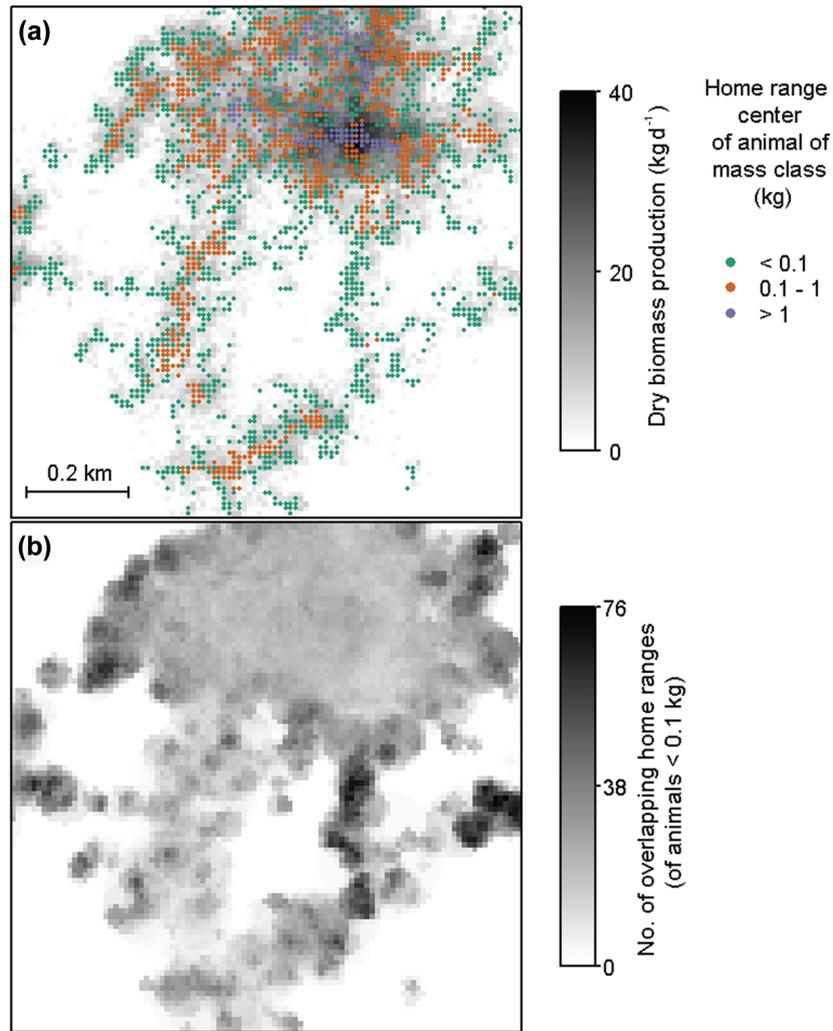


Figure 2. Spatial home range patterns in a resource-rich landscape section for one exemplary simulation of the allometric model (power-law input distribution with exponent of -1.2 , $\gamma_{PI} = 10 \times 10^{-2}$, $SATan = 0.9$). (a) The central home range cells of three body mass classes are plotted 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.

ranges at the periphery of large patches or in smaller patches (Fig. 2a). Consequently, the latter regions have a higher overlap of small animal home ranges (Fig. 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. 3a–b). These power-laws explain between 38% and 96% of the variance in log-transformed home range sizes. 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 analyzed over the whole range of body masses (Fig. 3a–c). Generally, lower saturation levels yield realistic home range scaling for scenarios with less steep input distributions (Fig. 3a). These scenarios, however, result in model communities with less steep body mass distributions compared to validation communities (Fig. 3c). The number of animals in the community is within reasonable ranges (13516 ± 1430 on 1 km^2 of suitable habitat; mean \pm 95% CI; comparable validation data are given in Table A2.3).

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. 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. 3a). Increased γ_{PI} , however, leads to decreasing home range sizes of all animals (i.e. reduces

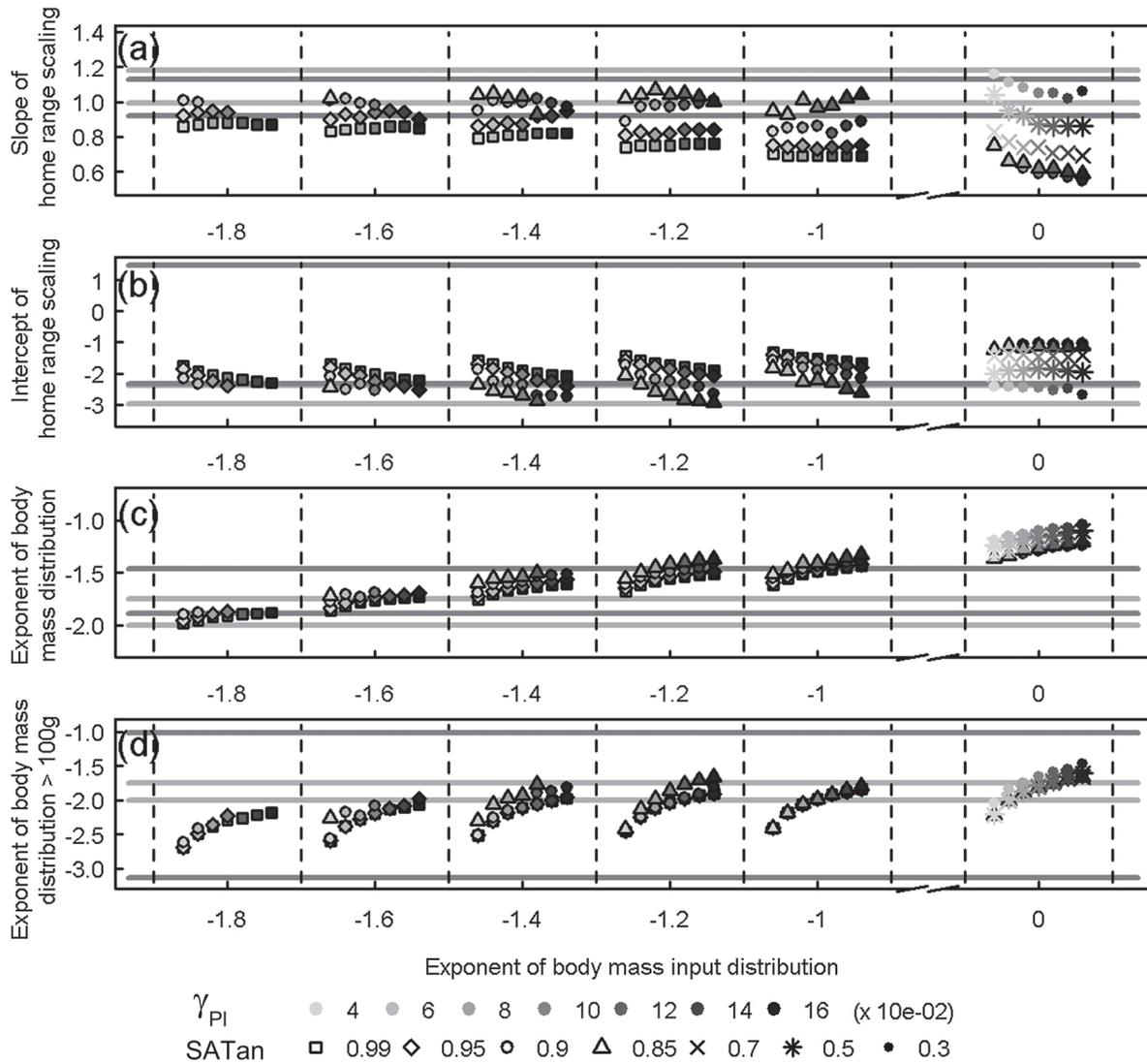


Figure 3. Scaling of home range size (a–b) and of individual abundance (ISD) (c–d) with body mass of the modelled mammal community. All results are shown as a function of different body mass input distributions, individual resource use (γ_{PI}) and saturation (SATan). Home range scaling analyzed by OLS regression of \log_{10} -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.

the intercept of the home range allometry) (Fig. 3b), and to less steep body mass distributions (i.e. shifts the community composition towards more large animals) (Fig. 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. 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 Fig. 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. 4). The model affects shallower input distributions more strongly than already steep input distributions. Figure 4 even suggests a non-linear relationship between this 'steepening effect' of the model and the slope of the input distribution.

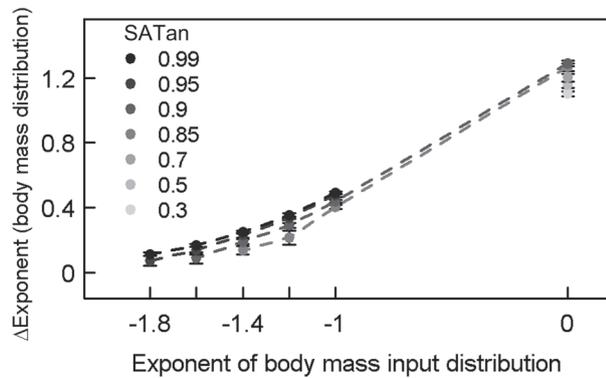


Figure 4. Effect the simulation model has on shaping the body mass distribution of the mammal community in dependence of the body mass input distribution. Values are the difference between the exponent of the body mass input distribution and the resulting body mass distribution. Results are shown exemplarily for different scenarios with γ_{PI} of 10×10^{-2} . Shades of grey indicate saturation levels. Error bars are 95% CI of the five landscape replicates of each scenario. Note that not all saturation levels could be achieved for all scenarios; for reasons see Supplementary material Appendix 1.

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. 3 and 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. 5a–c).

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 ($PC \times R$). 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. 6a–c).

Landscape and resource fragmentation rather strongly affect the slope of the home range allometry: strongly heterogeneous landscapes result in steeper home range scaling (Fig. 5d), 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. 6e–f).

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 1981b, 2007, Richie and Olf 1999, Carbone et al. 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). The presented model predicts spatially-explicit distributions of home ranges in animal communities (Fig. 2). Moreover, it predicts both realistic home range size - body mass relationships and realistic distributions of individual body mass (Fig. 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. 3, 5, 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. 3d). Moreover, the model also yields realistic prediction when applied to specific communities (Fig. 5).

Mechanisms and model behaviour

The response of the model output variables to changing levels of individual resource use (γ_{PI}) and saturation (SATan) (Fig. 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. 3b). High resource availability also facilitates the establishment of large animals which makes body mass distributions more shallow (Fig. 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. 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 result-

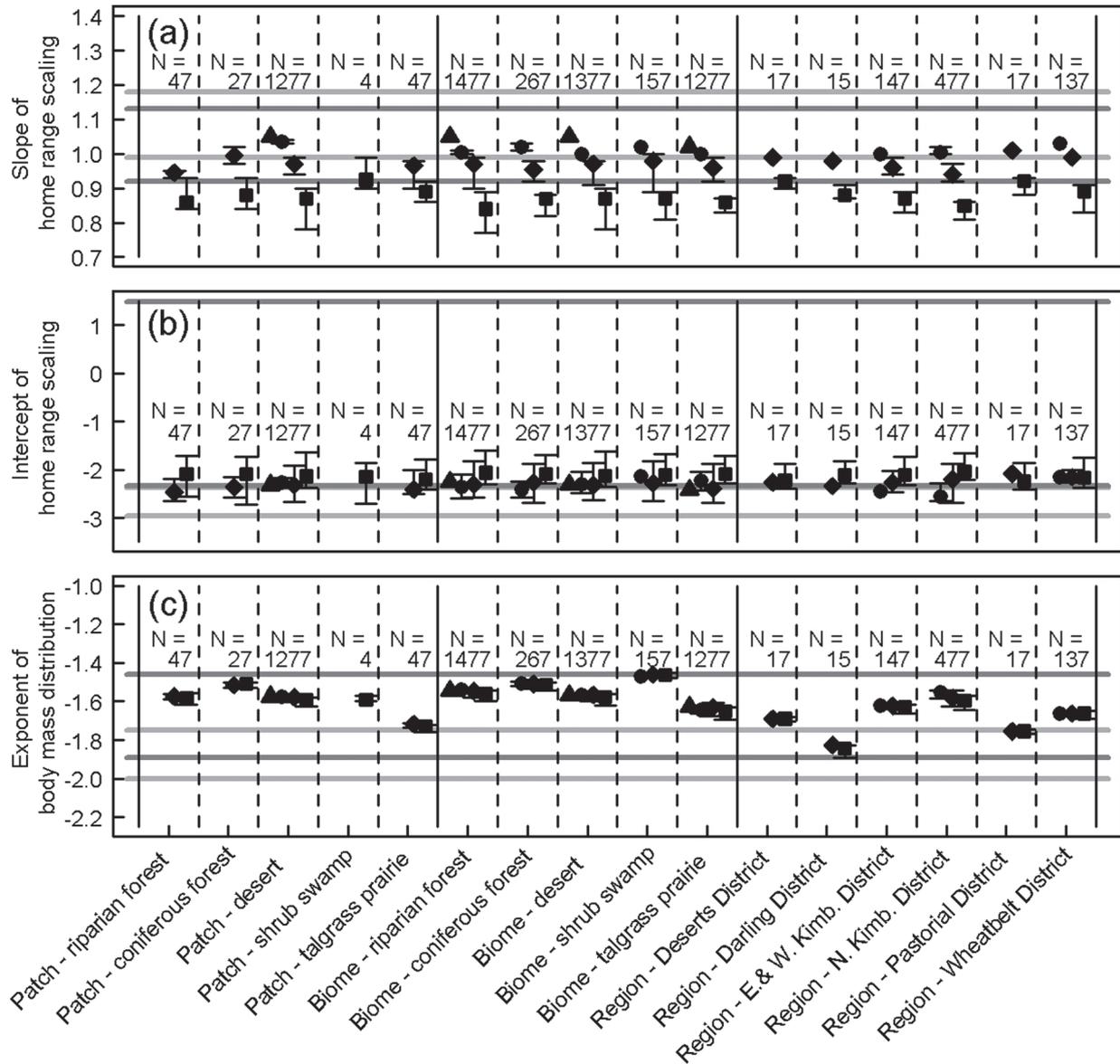


Figure 5. Simulation results of scenarios with empirical communities of different habitat types and different spatial scales as input distributions. These were achieved by combining, species data with an allometric relationship of population density (Methods). Symbols indicate saturation (square: $SAT_{an} = 0.99$, diamond: $SAT_{an} = 0.95$, circle: $SAT_{an} = 0.9$, triangle: $SAT_{an} = 0.85$). 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. 2. 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 $CFA > 2$ (Supplementary material Appendix 1).

ing home ranges of small animals are comparatively large. Therefore higher saturation results in (1) shallower slopes of the home range allometry (due to larger home range size of small individuals, Fig. 3a), (2) larger intercepts (due to generally larger home ranges when resource levels are reduced, Fig. 3b), and (3) a steeper body mass distribution (due to a higher proportion of small animals, Fig. 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.

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 meta-community, this raises questions about processes structuring regional

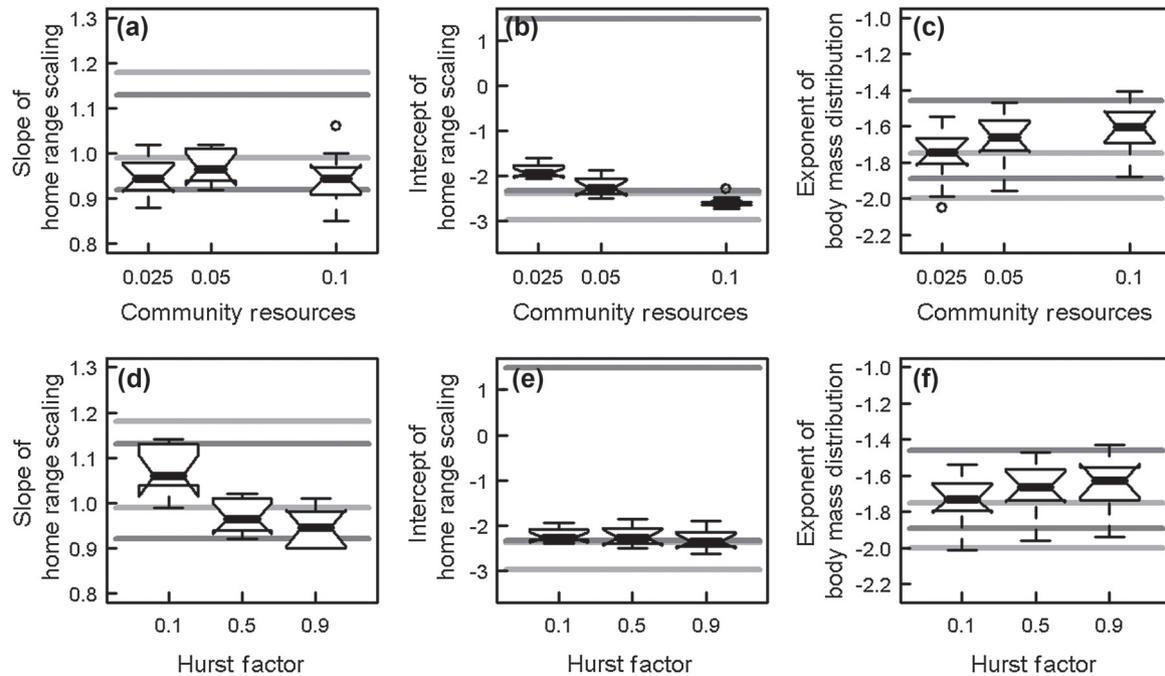


Figure 6. Test of the effects of changed resource production that is available to the community ($PC \times R$) in $\text{kg} \times \text{m}^{-2} \times \text{year}^{-1}$, and of the effect of changing heterogeneity of the landscape, i.e. the clumpiness of resources (Hurst-factor of 0.1 for strongly 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 Fig. 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% CI of the median, and small circles show outliers. Horizontal lines give the range of validation data. For details see caption of Fig. 2.

species pools and local communities. Understanding how meta-community 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 (Starzomsky 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. 3). In contrast, for steep input distributions community structure is dominated by regional mechanisms shaping the input distribution (Fig. 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).

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 foot-print of a species (Makarieva et al. 2005).

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.

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 (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).

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.

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- Supplementary material (available online as Appendix O18556 at <www.oikos.ekol.lu.se/appendix>. Appendix 1 and 2.