



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

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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.

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 (Bowers et al. 1996, 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. (2011) 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-explicit 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. (2011) 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.

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. 2011 and in Supplementary material Appendix 1, 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.

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 km²). For all simulations we used moderate autocorrelation ($H = 0.5$) and variance ($\sigma^2 = 30$) (Fig. 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. 2011).

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. 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 \times grid cell⁻¹ \times d⁻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. 2011 for analyses of the effects of landscape fragmentation and the share of resources that is available to the community).

Individual home range formation

Besides different sub-models of foraging movement included in this part of the model, individual home range formation is implemented as described in Buchmann et al. (2011). We therefore only provide a short model description here – a complete model description following the ODD protocol (Grimm et al. 2010) is provided in Supplementary material Appendix 1. 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 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. 2011, yielding realistic community structure).

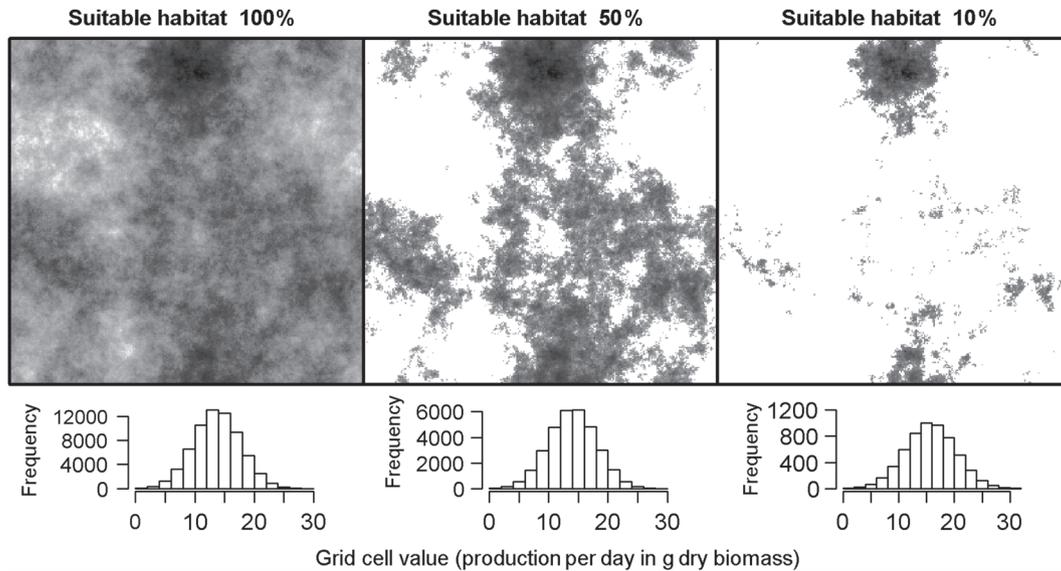


Figure 1. Two-dimensional illustration of fractal simulation landscapes (257×257 grid cells). Grey scale values show the daily resource production in a cell (from light grey to black, corresponding to -0.1 to ~ 30 g dry biomass, respectively). The landscapes (suitable area 100%) were ‘flooded’ (i.e. 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 rescaled to ensure that suitable cells in all habitat loss scenarios have the same relative frequency of resource production.

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 systematically 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 (Harestad and Bunnell 1979, Holling 1992, Haskell et al. 2002, Jetz et al. 2004, Buchmann et al. 2011). The coefficient of this scaling relationship is a model parameter (γ_{PI} , here $\gamma_{PI} = 4 \times 10^{-2}$) (for sensitivity analysis see Supplementary material Appendix 2).

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 Supplementary material Appendix 1 (‘7.3. submodel community saturation’) and Appendix 2, respectively, for simulation experiments we use $SAT = 0.95$).

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.

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. 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. 2011). 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.

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. 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.

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 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

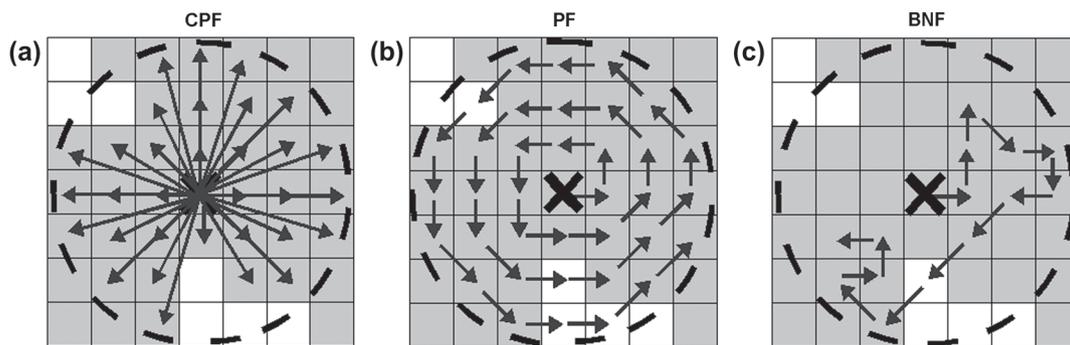


Figure 2. Schematic illustration of foraging and movement principles that are associated with three different foraging movement models. Length of arrows indicate the distance (DC) accounted for locomotion cost for the respective cells. White grid cell symbolize unsuitable habitat. (a) In the CPF movement 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).

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 (ΣDC) 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

$$DC = \frac{\text{daily accounted distance}}{\text{number of cells in home range}} \quad (1)$$

which translates in our modelling context to

$$DC = \frac{(875 \text{ m} \times M^{0.22})}{(1107 \text{ cells} \times M^{1.05})} = 0.79 \times M^{-0.83} \quad (2)$$

(in meter per cell, M in kg)

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 non-parametric 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). 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 Supplementary material Appendix 2).

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 Supplementary material Appendix 3 for sample distributions). It has been shown earlier (Buchmann et al. 2011) 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.

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. 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 ~ 250 th and the ~ 40 th 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 (Supplementary material Appendix 2). For further comparisons of empirical patterns and model predictions see Buchmann et al. (2011).

As expected, the composition of model communities changes with loss of suitable habitat and in dependence of the foraging movement model applied (Fig. 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. 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.

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. 5a–c, 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. 5c, 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

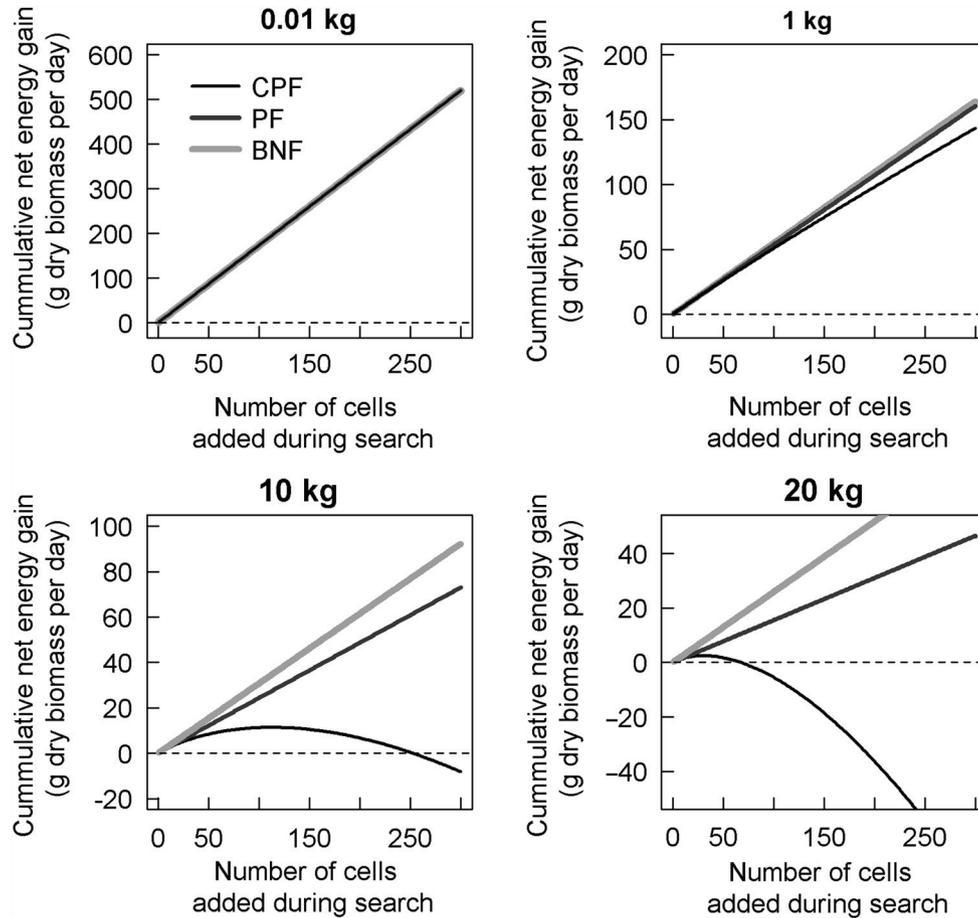


Figure 3. Cumulative net energy gain for the first 300 grid cells added during home range search for the three foraging movement approaches and different animal body masses. Results shown are model predictions for a single animal that is randomly located into a homogeneous resource landscape (suitable area of 100%, all cells with average resource production).

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)

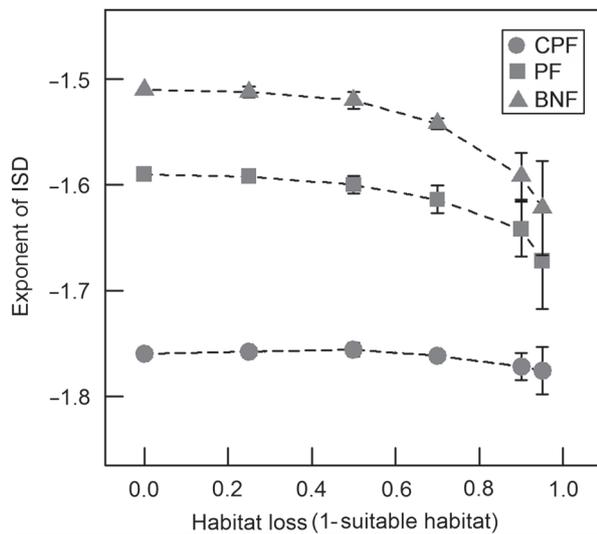


Figure 4. Exponent of the ISD of model communities, with three different foraging movement models. Grey symbols give means of five landscape replicates, error bars 95% CIs.

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).

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. 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.

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) on community structure (namely the ISD) and on the corresponding reaction of communities to habitat loss (Fig. 1). Generally, ISDs of terrestrial communities are not well

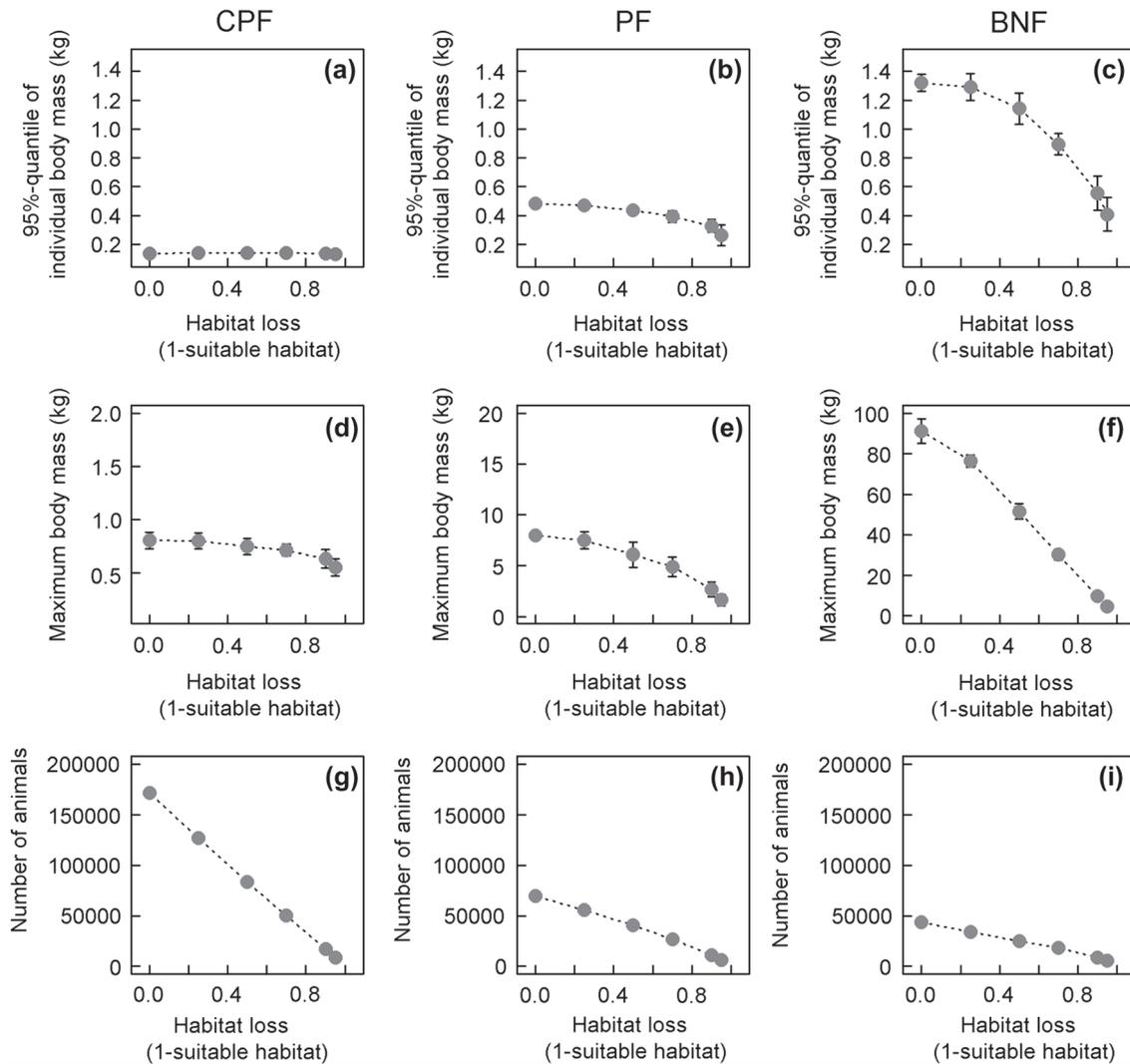


Figure 5. 95%-quantiles of body mass (a–c), maximum body mass (d–f, note different scaling of the y-axes), and number of animals of model communities (g–i) for three different foraging movement models (on the left side central place foragers, in the middle patrolling foragers and on the right side body mass dependent nomadic foragers). Circles give the means of five landscape replicates, error bars 95% CIs.

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. 2011). 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, May et al. 2009) this lack of data currently only allows to compare more general patterns such as the allometry of home range size (Supplementary material Appendix 2), 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. 2011 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. 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 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. 2011). 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. 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. 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 (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 extensions 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.

Conclusion

Although it is known that 1) 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 2) 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 (Börger et al. 2008, Van Moorter et al. 2009) could be integrated into the framework used here. These could also consider additional movement costs in fragmented landscapes such as 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. 2011) 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.

Acknowledgements – We thank J. Moloney for his support in implementing the model, various members from the research group Plant Ecology and Nature Conservation of the Univ. of Potsdam as well as J. Eccard and E. Rosmanith for helpful suggestions and ideas. CMB would like to thank the Graduate Initiative on Ecological Modelling of the Univ. of Potsdam for financial support. FJ and FMS acknowledge support from the European Union through Marie Curie Transfer of Knowledge Project FEMMES (MTKD-CT-2006-042261). RN gratefully acknowledges the Humboldt Foundation for the Friedrich Wilhelm Bessel Award that enabled this collaborative work, and the Israel Science Foundation (ISF-FIRST 1316/05), the US-Israel Binational Science Foundation (BSF 124/2004) and the Inst. for Advanced Studies in Jerusalem, for supporting his research on animal movement.

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Supplementary material (Appendix E6924 at <www.oikosoffice.lu.se/appendix>). Appendix 1–3.