Contents lists available at SciVerse ScienceDirect







journal homepage: www.elsevier.com/locate/ecolinf

# Habitat loss and fragmentation affecting mammal and bird communities—The role of interspecific competition and individual space use

Carsten M. Buchmann <sup>a,b,\*</sup>, Frank M. Schurr <sup>b</sup>, Ran Nathan <sup>c</sup>, Florian Jeltsch <sup>b</sup>

<sup>a</sup> Department of Computational Landscape Ecology, Helmholtz Centre for Environmental Research - UFZ, Permoserstr. 15, D-04318 Leipzig, Germany

<sup>b</sup> Department of Plant Ecology and Nature Conservation, Institute of Biochemistry and Biology, University of Potsdam, Maulbeerallee 2, D-14469 Potsdam, Germany

<sup>c</sup> Movement Ecology Laboratory, Department of Ecology, Evolution and Behavior, Alexander Silberman Institute of Life Sciences, The Hebrew University of Jerusalem,

Edmond J. Safra campus, Givat Ram, IL-91904 Jerusalem, Israel

## ARTICLE INFO

Article history: Received 10 January 2012 Accepted 30 November 2012 Available online 13 December 2012

Keywords: Allometry Body size Fractal landscapes Foraging movement Individual-based model Locomotion costs

## ABSTRACT

Fragmentation and loss of habitat are major threats to animal communities and are therefore important to conservation. Due to the complexity of the interplay of spatial effects and community processes, our mechanistic understanding of how communities respond to such landscape changes is still poor. Modelling studies have mostly focused on elucidating the principles of community response to fragmentation and habitat loss at relatively large spatial and temporal scales relevant to metacommunity dynamics. Yet, it has been shown that also small scale processes, like foraging behaviour, space use by individuals and local resource competition are also important factors. However, most studies that consider these smaller scales are designed for single species and are characterized by high model complexity. Hence, they are not easily applicable to ecological communities of interacting individuals. To fill this gap, we apply an allometric model of individual home range formation to investigate the effects of habitat loss and fragmentation on mammal and bird communities, and, in this context, to investigate the role of interspecific competition and individual space use. Results show a similar response of both taxa to habitat loss. Community composition is shifted towards higher frequency of relatively small animals. The exponent and the 95%-quantile of the individual size distribution (ISD, described as a power law distribution) of the emerging communities show threshold behaviour with decreasing habitat area. Fragmentation per se has a similar and strong effect on mammals, but not on birds. The ISDs of bird communities were insensitive to fragmentation at the small scales considered here. These patterns can be explained by competitive release taking place in interacting animal communities, with the exception of bird's buffering response to fragmentation, presumably by adjusting the size of their home ranges. These results reflect consequences of higher mobility of birds compared to mammals of the same size and the importance of considering competitive interaction, particularly for mammal communities, in response to landscape fragmentation. Our allometric approach enables scaling up from individual physiology and foraging behaviour to terrestrial communities, and disentangling the role of individual space use and interspecific competition in controlling the response of mammal and bird communities to landscape changes. © 2013 Elsevier B.V. All rights reserved.

## 1. Introduction

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

Even though differences in methodology and terminology in various studies cause difficulties to synthesise general conclusions (Fahrig, 2003), effects of reduced habitat area (habitat loss) on populations are relatively consistent among studies and rather well understood. A large number of studies report threshold behaviour (so called 'extinction thresholds') of animal populations with reduced amount of habitat, and several theoretical modelling studies have proposed a variety of mechanistic explanations for such non-linear dynamics, ranging from percolation theory and isolation effects to time lag and Allee effects (Bascompte and Sole, 1996; Fahrig, 2002; Harrison and Bruna, 1999; Swift and Hannon, 2010). In contrast, reported effects of fragmentation per se on populations are less clear and often even contradictory (compared to the effects of habitat loss). Fragmentation per se here means

<sup>\*</sup> Corresponding author at: Department of Computational Landscape Ecology, Helmholtz Centre for Environmental Research - UFZ, Permoserstr. 15, D-04318 Leipzig, Germany. Tel.: +49 341 235 1951; fax: +49 341 235 1939.

E-mail address: carsten.buchmann@ufz.de (C.M. Buchmann).

<sup>1574-9541/\$ –</sup> see front matter © 2013 Elsevier B.V. All rights reserved. http://dx.doi.org/10.1016/j.ecoinf.2012.11.015

the spatial configuration of habitat only while total habitat area remains unchanged (this aspect was also intensively discussed in the 'SLOSS debate', e.g. Wilcox and Murphy, 1985 and the references therein). Different studies report positive or negative effects of fragmentation on species occurrence or abundance, but some also report no effect (Fahrig, 2003; Smith et al., 2011). The interplay of habitat fragmentation with habitat loss (for example how fragmentation affects the threshold behaviour with habitat loss, or how total habitat area controls the strength of the fragmentation effect) still poses a particularly difficult challenge to scientists and conservation managers.

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

Processes at small scales, such as foraging behaviour, space use and local resource competition, however, play a crucial role in how individuals and species in interacting communities cope with heterogeneous resource distributions (Buchmann et al., 2012; Debinski and Holt, 2000; Gautestad and Mysterud, 2010; Hawkes, 2009; Morales et al., 2010; Nee and May, 1992; Pita et al., 2010; Ritchie, 1998; Smith et al., 2011). Different space use behaviours of individuals of different taxa-for example the higher mobility and larger home ranges of birds compared to mammals (Breitbach et al., 2010; Ottaviani et al., 2006)-can also affect the response of communities to changes in resource distributions. Nevertheless, theoretical studies investigating such small scale mechanisms (e.g. optimal foraging behaviour, Nonaka and Holme, 2007; Skorka et al., 2009, but also Gautestad and Mysterud, 2010), have generally not made the step to consider species interactions, implying they are not yet geared towards exploring community questions. The main reason might be that studies accounting for the importance of individual behaviour and space use are too complex (Nonaka and Holme, 2007; Van Moorter et al., 2009) and often designed for a specific single species (e.g. Bowers et al., 1996; Skorka et al., 2009). We have recently proposed a simple alternative, an individual-based spatially explicit model of individual home range formation of multiple mammal species parameterized by allometric relationships (Buchmann et al., 2011, 2012). This approach considers the important role of individual space use and resource competition on home range formation (e.g. Nee and May, 1992; Pita et al., 2010; Swihart et al., 1988), thereby enabling mechanistic investigation of the processes structuring animal communities.

In this study we use a modification of the model described in Buchmann et al. (2012) to elaborate the role of interspecific competition and individual space use for communities facing landscape changes. In addition to mammals, we also parameterize the model for the first time for birds and explore how not only habitat loss, but also fragmentation (and the combination of both), affect the body mass distribution of these communities.

## 2. Methods

Our modelling study aims to explore the response of the body mass distribution—namely the individual size distribution (ISD, after White et al., 2007)-of mammal and bird communities to habitat loss and fragmentation, emphasising the role of interspecific competition and individual space use. In the Methods section we first explain the generation of simulation landscapes (including loss and fragmentation of habitat) followed by a brief description of the allometric model of home range formation for mammals and birds consuming primary production (i.e. herbivores and primarily herbivorous omnivores) and a description of how we use it to model community assembly. Here, we use a modification of the original model of Buchmann et al. (2011), namely a slightly more complex submodel for the calculation of movement cost. Originally we introduced this modification in a study that focussed particularly on the effects of different assumptions on movement strategies for communities (Buchmann et al., 2012). This movement model was chosen here because it additionally considers body mass dependence of movement distances, is therefore more closely oriented towards movement data, and hence, seems more appropriate for the investigation of communities with a large range of body mass.

## 2.1. Simulation landscapes

The well established and tested midpoint displacement algorithm (Hargrove et al., 2002; Jeltsch et al., 2011; Körner and Jeltsch, 2008; Saupe, 1988) was used to create fractal landscapes of  $257 \times 257$  cells, each interpreted as  $10 \times 10$  m, resulting in landscapes of ~6.6 km<sup>2</sup>. Using this approach, landscape fragmentation can be controlled by the Hurst-factor H, describing the spatial autocorrelation of grid cell values, interpreted as resource productivity. In simulations we used H = 0.1 for strongly fragmented, H=0.5 for intermediate and H=0.9 for weakly fragmented resource landscapes ( $\sigma^2$ , the variance in displacement of points, was set to 0.3 for all scenarios). To simulate habitat loss, grid cells with the lowest values, interpreted as resource productivity, were then set to 0 (i.e. to no resource productivity) until a certain share of habitat S was left as productive (i.e. suitable) habitat. In simulations S was set to 1.0, 0.75, 0.5, 0.3, 0.1 and 0.05. To ensure comparability between scenarios and avoid landscape artefacts, landscapes were rescaled using a rank-based transformation in order to achieve all landscapes having the same normal distribution of grid-cell values (mean and S.D.) as the landscapes with S = 1.0. Additionally all landscapes were scaled to have an average resource productivity in productive cells of  $6.85 \times 10^{-2}$  kg dry biomass  $\times$  grid cell<sup>-1</sup>  $\times$  day<sup>-1</sup>, a value oriented towards the productivity of typical shrub lands and grasslands (Whittaker, 1975). Only 20% of this primary production is assumed to be available to the mammal or the bird community considering competition with other taxa and because not all plant material is consumable (see Buchmann et al., 2011 for systematic variation of this value). The resource is, however, not further specified, hence we model a simplified community in which all individuals consume and compete for this single type of resource.

#### 2.2. Model of individual home range formation of mammals and birds

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

Doing so assures that the total costs for the sum of all home range cells correspond approximately to data on individual daily movement distance. Both, average movement distance and average home range size, are derived from empirical allometric relations (see later and Buchmann et al., 2012).

If sufficient resources can be achieved to match the individual's daily resource requirements without the necessary area exceeding either the landscape size or a mass-specific maximum home range size, the search is considered successful. After testing all suitable cells as potential core cells, and if at least one of these searches was successful, the animal chooses the smallest, i.e. the most efficient, home range. Fig. 1 illustrates principles of the individual home range search and how it leads to a community of interacting individuals with overlapping home ranges in space.

Since individuals are characterized by their body mass, all model parameters related to this model compartment can be parameterized by allometric relationships. Here only the sources and/or the derivation of used allometric relationships are given (see Buchmann et al., 2011 and, for the approach to calculate movement costs, see Buchmann et al., 2012).

Daily energy requirements of individuals are determined after the allometric equations of field feeding rate for mammals and birds, given in Nagy (2001), and the locomotion cost per distance is calculated after equations reported by Calder (1996). For the calculation of the costs involved in adding new cells to a potential home range we need allometric relationships for daily movement distance and for average home range size (see above). For mammals we use an allometric relationship of daily movement distance for non-carnivorous mammals, reported by Garland (1983) (see Fig. 1). Comparable data on daily movement distance are, to our knowledge, not available for birds. Sutherland et al. (2000) found that the allometry of natal dispersal distance has the same slope for birds and mammals; the coefficient is, however, 10 times higher for birds. As a first approximation we assume that this result characterizes general differences in movement behaviour between mammals and birds (i.e. a generally 10 times higher mobility in birds). We thus applied the mammal equation for daily movement distance from Garland (1983) multiplied by 10 for birds, as our yet-to-be-confirmed assumption. As an estimate for average home range size we apply a combination of different empirically observed allometric relationships for birds and mammals (Bowman, 2003; Harestad and Bunnell, 1979; Holling, 1992; Ottaviani et al., 2006). In order to then balance energetic costs of movement with resource use, these costs were converted into dry biomass equivalent by a factor given in Nagy (2001) for non-fermenting consumption of plant diet. The allometric relationship for maximum home range size for mammals is calculated as the combination of maxima of constraint spaces for home range size of herbivores and omnivores reported by Kelt and Van Vuren (2001). Since no comparable data are available for birds, we re-analysed data from Ottaviani et al. (2006) on non-defended feed-ing areas of omnivorous birds (because omnivores generally have larger home ranges than herbivores, birds as well as mammals, e.g. Harestad and Bunnell, 1979; Holling, 1992; Ottaviani et al., 2006) using quantile regression (with R package 'quantreg', Koenker, 2009; R Development Core Team, 2008) on log-transformed data. The back transformed (antilog) equation corresponding to the 95%-quantile is used as an estimate of maximum home range size for birds.

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

#### 2.3. Community assembly and analysis of simulation output

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



**Fig. 1.** Schematic illustration of major model mechanisms of the allometric community model of individual home range formation. On the left, a section of a simulation landscape with some overlapping home ranges is shown (resource productivity is indicated as grey scale values, home ranges as circles). For two of these home ranges (a small one of a small individual, and a larger one of a larger individual) exemplary movement paths are illustrated, which could be represented by the approach used to calculate movement costs. Note that smaller animals visit a higher proportion of home range cells on a daily basis than do larger animals because daily movement distance scales with ~0.25, whereas home range scarch the energy balance of each home range cell is calculated on a daily basis, as shown on the right side.

distribution (mammals: 0.01–0.02, 3–5, 20–30 and 50–75 kg, birds: 0.01–0.02, 1–2, 3–5 and 12–18 kg).

Simulations were stopped when a certain share of community resources were consumed by the individuals, which reflects certain community saturation. To determine this specific resource level, the different scenarios were initially run until 5000 individuals consecutively failed in establishing a home range. The amount of resources consumed by the community at this stage was then interpreted as 100% (full community saturation). This assumption is justified because even for much smaller number of consecutively failing animals the overall amount of consumed resources changed very little. Knowing the resource level corresponding to 100% community saturation then allowed us to stop each simulation at a defined community saturation (SAT) via the actual level of community resource consumption. Here we use SAT = 0.95, a value resulting in realistic communities.

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

## 3. Results

The distribution of individual body mass (ISD) showed a strong response to habitat loss (less suitable habitat area S) and fragmentation (spatial configuration of remaining habitat, controlled by the Hurst-factor H). However, the response was different for mammal and bird communities (Fig. 2a, b and c, d, respectively). For both taxa, habitat loss of up to 25% (100% to 75% suitable habitat area) does not significantly alter the ISD (indicated by the ISD exponent) or the size of the largest individuals (indicated by the 95%-quantile of body mass) in the community. The zone of relatively low impact extends to ~70% habitat loss in birds, but not in mammals particularly in highly fragmented landscapes (H=0.1). Here, a strong shift to higher frequency of relatively small animals (Fig. 2a and c), and to a reduced size of the largest individuals in the community (Fig. 2b and d) occurs. This shift, occurring at more severe cases of habitat loss also in bird communities, exhibits non-linear threshold behaviour with increasing habitat loss, but more profoundly in mammals than in birds. Fragmentation per se (i.e. the same habitat area) hardly has any effect on the response to habitat loss in bird communities. Mammal communities, however, exhibit strong response: fragmentation here adds to the effect of habitat loss and vice versa.

The basic effects of habitat loss, i.e. less suitable habitat area, on the community body mass distribution can be explained by taking a closer look at narrower mass windows of the mammal community (Fig. 3a–d). Such smaller body mass ranges could be interpreted to represent populations of single species and are therefore hereafter referred to as 'populations'. The size of these populations decreases with habitat loss, however, the reduction of abundance deviates considerably from a linear decrease (Fig. 3e–h). The largest species is affected strongly even when 75% habitat is available and the abundance is below the abundance corresponding to a linear decrease for all levels of habitat area. When each mass class is simulated in isolation also smaller species show this response to habitat loss (Fig. 3i–1).



**Fig. 2.** Effect of habitat loss and fragmentation on the community body mass distribution, specifically the individual size distribution ISD. Changes of the exponent, and of the 95%-quantile of this distribution are shown for mammal and bird communities. Mean +/-95% C.I.s of five landscape replicates; grey scale values symbolize landscape fragmentation, see legend.



**Fig. 3.** Effect of habitat loss on the number of mammals in narrower mass ranges (representing populations of certain species). Population size of these populations in mammal communities is shown in dependence of the amount of suitable habitat (a–d). The thin dashed lines connect the population size at highest and lowest habitat area, i.e. they denote a linear decrease of population size with habitat loss. The deviation of population size from this linear decrease is shown in the middle row (e–h). Below (i–l), the deviation from a linear decrease of population size with habitat loss for simulations of the populations alone, i.e. without competition with individuals outside the respective mass range, is shown. Mean +/-95% C.I.s of five landscape replicates with intermediate fragmentation (H = 0.5).

However, when simulated together with the entire community (i.e. under interspecific competition), the smaller species even profit from habitat loss, relative to the linear decrease of abundance. There is the trend that for smaller species the range of suitable habitat levels with which a species 'profits' is shifted to less habitat (Fig. 3e–g). These findings reflect the role of competition in explaining the non-linear response of the ISD exponent. This pattern was broadly similar for birds.

In contrast to habitat loss, which has a similar effect on mammal and bird communities, fragmentation disproportionately affects mammals compared to birds (Fig. 2a and b). The importance of interspecific competition for the observed strong effect of fragmentation on mammal communities can be demonstrated by considering a population of small mammals (0.01–0.02 kg) at different levels of fragmentation. When this population is simulated without interspecific competition, fragmentation decreases population size (Fig. 4a). This effect is rather weak. However, if the response of this population is observed in the community context (i.e. simulated in competition with all other body masses) the effect of fragmentation is reversed, and stronger relative to population size (Fig. 4b). Now, the abundance of this small-bodied population is increased with increasing fragmentation.

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

The allometry of home range size in simulated communities also shows a different response to decreasing suitable habitat and fragmentation between mammals and birds (Fig. 6a and b compared to c and d).



**Fig. 4.** Effect of habitat loss and fragmentation on the number of mammals in a smaller body size range (0.01–0.02 kg), at different levels of suitable habitat, simulated alone (a) and in competition with the entire mammal community (b). Mean +/-95% C.I.s of five landscape replicates; grey scale values symbolize landscape fragmentation: light grey for strongly fragmented (H=0.1) and black for weakly fragmented (H=0.9) habitat. Insets show the absolute difference between the number of animals in strongly and weakly fragmented landscapes, i.e. the 'absolute fragmentation effect'.

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

## 4. Discussion

To our knowledge, this is the first explanation of how habitat loss and fragmentation affect the individual size distribution (ISD) of mammal and bird communities in terrestrial systems. In contrast to aquatic



**Fig. 5.** 'Relative fragmentation effect' on mammal and bird populations with interspecific competition. The relative fragmentation effect is the relative difference between the number of individuals in strongly and weakly fragmented landscapes ((#(H=0.1) - #(H=0.9))/#(H=0.9)), here shown for two body size ranges in either mammal or bird communities. Mean +/-95% C.Ls of five landscape replicates.



Fig. 6. Effect of habitat loss and fragmentation on the parameters of the allometry of home range size of the mammal and bird communities. Mean +/-95% C.I.s of five landscape replicates; grey scale values symbolize landscape fragmentation, see legend.

systems, the mechanisms that control body mass distributions, and how these mechanisms are affected by environmental change, are still largely unexplored in terrestrial communities (White et al., 2007). Our mechanistic model of individual home range formation in animal communities enables explicit exploration of the role of two important small scale mechanisms—individual space use and resource competition—in controlling the response of mammal and bird communities to habitat loss and fragmentation.

## 4.1. Effects of habitat loss on mammal and bird communities

Model predictions with respect to habitat loss (less suitable habitat area) agree for mammals and birds in demonstrating a shift to higher frequency of smaller and lower frequency of larger individuals. This is reflected in steeper ISDs and smaller size of the largest individuals in the community. Higher vulnerability of larger individuals to habitat loss has been reported in previous studies and was often related to their lower abundance (Belovsky, 1987; Ewers and Didham, 2006; Gaston and Blackburn, 1996; Harrison and Bruna, 1999, but see Henle et al., 2004). The limitation of home range establishment of the individuals of a species (i.e. that no home range can be found) is likely to be linked to the probability of local extinction of that species in the longer term. Hence, both the lower abundance and the higher extinction risk of larger animals are reflected in our simulation results.

The response of the ISD (exponent and 95%-quantile) shows, however, a non-linear response to habitat loss, namely only a strong reaction after some critical threshold of remaining habitat area has been reached. Critical (extinction) thresholds have been described and reviewed repeatedly in connection with habitat loss (e.g. Fahrig, 2003; Swift and Hannon, 2010). These thresholds typically range in similar magnitudes of habitat loss as those predicted by our model for the ISD exponent. The threshold response of the ISD exponent to habitat loss can be explained when observing different smaller mass windows (populations) in the community. When large species decline in abundance or even 'go extinct' with decreasing habitat area, resources become available to (the next) smaller species. This species can therefore compensate some of the negative effects of habitat loss on their abundance. The ISD exponent thus initially remains relatively unaffected with decreasing habitat, even if the 95%-quantile already is reduced. This effect of competitive release (Larsen et al., 2008; Thompson and Fox, 1993) resembles the phenomenon of mesopredator release reported for carnivores (Crooks and Soulé, 1999) and could thus be termed 'mesocompetitor-release'. To our knowledge, this phenomenon has not yet been reported for herbivore communities, and its existence therefore remains to be tested for empirically.

#### 4.2. Effects of habitat fragmentation

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

In mammal communities the allometry of home range is considerably less sensitive to fragmentation than in bird communities (compare McCann and Benn, 2006; Said et al., 2009, but see Selonen et al., 2001). This indicates their weaker potential to buffer fragmentation effects on community composition via individual space use. Consequently, changing abundance and competitive release become the relevant mechanisms controlling mammal community response to fragmentation. We have shown that a population of very small mammals suffers from fragmentation in the absence of interspecific competition, comparable to the findings of a conceptual study not considering species interactions (Flather and Bevers, 2002). However, in the presence of interspecific competition such a population might even benefit from fragmentation that has a stronger impact on larger animals.

## 4.3. Model shortcomings and future directions

Our study considers small scale fragmentation at the scale of foraging areas (according to Smith et al., 2011). Large scale fragmentation can of course cause additional effects that we did not address. Isolation, for example, might affect small individuals in particular (Brown, 2007; Flather and Bevers, 2002). Moreover, factors related to population dynamics, like longer life span of larger animals or faster recovery related to shorter generation times of smaller individuals (Wissel et al., 1994), are not considered in our framework. Neither do we consider the possibility that individuals respond to landscape changes by changing the shape of their home range. One could also expect the higher energy expenditure of birds in larger home ranges in fragmented landscapes to decrease reproductive output (Hinsley, 2000). Other factors that are important to be considered for effective conservation planning are matrix (Prugh et al., 2008) and edge effects-the latter particularly for birds that often suffer from increasing nest predation rates at edges of habitat patches (Fletcher et al., 2007; Lindell et al., 2007). The combination of these possible additional factors could also cause behavioural changes such as increased territoriality (Banks et al., 2007; Ims et al., 1993). This complexity of factors and mechanisms demonstrates that our results cannot resolve the complete story of community response at all relevant scales. However, we have for the first time investigated the relevance of small scale mechanisms at the individual level for terrestrial communities experiencing landscape changes. Future work should therefore combine large scale metacommunity models with individual based modelling of relevant small scale mechanisms, like our optimal foraging based home range approach (see also Hawkes, 2009). For further refinements of the movement model and validation of predicted patterns, appropriate data at the community scale are required. In particular, multi-species abundance data for communities in differently fragmented habitats can allow for testing the relevance of the mesocompetitor-release phenomenon revealed by our model. Simulation results indicate that future empirical work focussing on species with a wide range of different body masses and different taxonomic groups (like mammals and birds) could contribute to a better mechanistic understanding of animal communities facing environmental change. Moreover, more refined movement data in general and for estimating the allometry of daily movement distance in particular seem to be of high importance to tighten the link between model results and real communities.

## 5. Conclusions

Using allometric relationships to combine resource competition and space use, considering individual physiology and foraging behaviour, our model predicts both common and distinct patterns of community response to habitat loss and fragmentation for mammals and birds. Our results have direct implications for community conservation based on habitat management: Firstly, the findings emphasize that mammals are particularly sensitive to a combination of habitat loss and habitat fragmentation, whereas birds are strongly affected only by habitat loss and can compensate for the negative effects of fragmentation by flexible individual space use enabled by their higher mobility. In the context of the SLOSS debate (Wilcox and Murphy, 1985 and the references therein) our results suggest taxon-specific differences: while mammals depend on large patches (SL), birds can also cope with many small patches (SS). Secondly, we show that competitive release in mammal communities can mask negative effects of landscape changes on smaller species. This should be considered in future conservation-oriented monitoring and the evaluation of conservation measures. Overall, we propose an allometric approach to address the challenging scaling-up problem of linking individuals to communities, and, more specifically, highlight the importance of considering the role of movement capacity of individuals and interspecific competition in shaping animal response to habitat loss and fragmentation.

## Acknowledgements

We thank N. Blaum and E. Rosmanith and various members from the research group Plant Ecology and Nature Conservation of the University of Potsdam for helpful suggestions and ideas, as well as D. Ottaviani for providing us with her data on bird body masses and home ranges for re-analysis. C. Buchmann would like to thank the Graduate Initiative on Ecological Modelling ('UpGrade') of the University of Potsdam for financial support, F. Jeltsch and F. Schurr acknowledge support from the European Union through Marie Curie Transfer of Knowledge Project FEMMES (MTKD-CT-2006-042261). R. Nathan 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 and ISF 1259/09), the US-Israel Binational Science Foundation (BSF 124/2004 and 255/2008), the German-Israeli Foundation (GIF 999–66.8/2008), the German–Israeli Project Cooperation (DIP NA 846/1-1), and Adelina and Massimo DellaPergola Chair of Life Sciences, for supporting his research on animal movement.

#### References

- Banks, S.C., Piggott, M.P., Stow, A.J., Taylor, A.C., 2007. Sex and sociality in a disconnected world: a review of the impacts of habitat fragmentation on animal social interactions. Canadian Journal of Zoology 85, 1065–1079.
- Bascompte, J., Sole, R.V., 1996. Habitat fragmentation and extinction thresholds in spatially explicit models. Journal of Animal Ecology 65, 465–473.
- Belovsky, G.E., 1987. Extinction models and mammalian persistence. In: Soulé, M.E. (Ed.), Viable Populations for Conservation. Cambridge University Press, Cambridge, pp. 35–57.
- Bowers, M.A., Matter, S.F., Dooley, J.L., Dauten, J.L., Simkins, J.A., 1996. Controlled experiments of habitat fragmentation: a simple computer simulation and a test using small mammals. Oecologia 108, 182–191.
- Bowman, J., 2003. Is dispersal distance of birds proportional to territory size? Canadian Journal of Zoology 81, 195–202.
- Breitbach, N., Laube, I., Steffan-Dewenter, I., Böhning-Gaese, K., 2010. Bird diversity and seed dispersal along a human land-use gradient: high seed removal in structurally simple farmland. Oecologia 162, 965–976.
- Brown, W.P., 2007. Body mass, habitat generality, and avian community composition in forest remnants. Journal of Biogeography 34, 2168–2181.
- Buchmann, C.M., Schurr, F.M., Nathan, R., Jeltsch, F., 2011. An allometric model of home range formation explains the structuring of animal communities exploiting heterogeneous resources. Oikos 120, 106–118.
- Buchmann, C.M., Schurr, F.M., Nathan, R., Jeltsch, F., 2012. Movement upscaled—the importance of individual foraging movement for community response to habitat loss. Ecography 35, 436–445.
- Calder, W.A.I.I.I., 1996. Size, Function, and Life History. Dover Publishers Inc., Mineola, New York.
- Chatterjee, S., Templin, R.J., Campbell, K.E., 2007. The aerodynamics of Argentavis, the world's largest flying bird from the Miocene of Argentina. Proceedings of the National Academy of Sciences of the United States of America 104. 12398–12403.
- Crooks, K.R., Soulé, M.E., 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400, 563–566.

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

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

- Fahrig, L, 2002. Effect of habitat fragmentation on the extinction threshold: a synthesis. Ecological Applications 12, 346–353.
- Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34, 487–515.
- Flather, C.H., Bevers, M., 2002. Patchy reaction-diffusion and population abundance: the relative importance of habitat amount and arrangement. American Naturalist 159, 40–56.
- Fletcher, R.J., Ries, L., Battin, J., Chalfoun, A.D., 2007. The role of habitat area and edge in fragmented landscapes: definitively distinct or inevitably intertwined? Canadian Journal of Zoology 85, 1017–1030.
- Garland, T., 1983. Scaling the ecological cost of transport to body mass in terrestrial mammals. American Naturalist 121, 571–587.
- Gaston, K.J., Blackburn, T.M., 1996. Conservation implications of geographic range size body size relationships. Conservation Biology 10, 638–646.
- Gautestad, A.O., Mysterud, I., 2010. Spatial memory, habitat auto-facilitation and the emergence of fractal home range patterns. Ecological Modelling 221, 2741–2750.
- Harestad, A.S., Bunnell, F.L., 1979. Home range and body weight—reevaluation. Ecology 60, 389–402.
- Hargrove, W.W., Hoffman, F.M., Schwartz, P.M., 2002. A fractal landscape realizer for generating synthetic maps. Conservation Ecology 6 (2) (http://www.consecol. org/vol6/iss1/art2).
- Harrison, S., Bruna, E., 1999. Habitat fragmentation and large-scale conservation: what do we know for sure? Ecography 22, 225–232.
- Haskell, J.P., Ritchie, M.E., Olff, H., 2002. Fractal geometry predicts varying body size scaling relationships for mammal and bird home ranges. Nature 418, 527–530.
- Hawkes, C., 2009. Linking movement behaviour, dispersal and population processes: is individual variation a key? Journal of Animal Ecology 78, 894–906.
- Henle, K., Davies, K.F., Kleyer, M., Margules, C., Settele, J., 2004. Predictors of species sensitivity to fragmentation. Biodiversity and Conservation 13, 207–251.
- Hinsley, S.A., 2000. The costs of multiple patch use by birds. Landscape Ecology 15, 765–775.
- Holling, C.S., 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. Ecological Monographs 62, 447–502.
- Ims, R.A., Rolstad, J., Wegge, P., 1993. Predicting space use responses to habitat fragmentation: can voles *Microtus oeconomus* serve as an experimental model system (EMS) for capercaillie grouse *Tetrao urogallus* in boreal forest. Biological Conservation 63, 261–268.
- Jeltsch, F., Moloney, K.A., Schwager, M., Körner, K., Blaum, N., 2011. Consequences of correlations between habitat modifications and negative impact of climate change for regional species survival. Agriculture, Ecosystems and Environment 145, 49–58.
- Jetz, W., Carbone, C., Fulford, J., 2004. The scaling of animal space use. Science 306, 266–268.
- Kareiva, P., Mullen, A., Southwood, R., 1990. Population dynamics in spatially complex environments: theory and data. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 330, 175–190.
- Kelt, D.A., Van Vuren, D.H., 2001. The ecology and macroecology of mammalian home range area. American Naturalist 157, 637–645.
- Koenker, R., 2009. Quantreg: Quantile Regression. (R package version 4.30. http:// www.R-project.org).
- Körner, K., Jeltsch, F., 2008. Detecting general plant functional type responses in fragmented landscapes using spatially-explicit simulations. Ecological Modelling 210, 287–300.
- Körner, K., Treydte, A., Burkart, M., Jeltsch, F., 2010. Simulating direct and indirect effects of climatic changes on rare perennial plant species in fragmented landscapes. Journal of Vegetation Science 21, 843–856.
- Larsen, T.H., Lopera, A., Forsyth, A., 2008. Understanding trait-dependent community disassembly: dung beetles, density functions, and forest fragmentation. Conservation Biology 22, 1288–1298.
- Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M., Gonzalez, A., 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7, 601–613.
- Lindell, C.A., Riffell, S.K., Kaiser, S.A., Battin, A.L., Smith, M.L., Sisk, T.D., 2007. Edge responses of tropical and temperate birds. Wilson Journal of Ornithology 119, 205–220.
- McCann, K.I., Benn, G.I., 2006. Land use patterns within Wattled Crane (Bugeranus carunculatus) home ranges in an agricultural landscape in KwaZulu-Natal, South Africa. Ostrich 77, 186–194.

- Mitchell, M.S., Powell, R.A., 2004. A mechanistic home range model for optimal use of spatially distributed resources. Ecological Modelling 177, 209–232.
- Morales, J.M., Moorcroft, P.R., Matthiopoulos, J., Frair, J.L., Kie, J.G., Powell, R.A., Merrill, E.H., Haydon, D.T., 2010. Building the bridge between animal movement and population dynamics. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 365, 2289–2301.
- Nagy, K.A., 2001. Food requirements of wild animals: predictive equations for freeliving mammals, reptiles, and birds. Nutrition Abstracts and Reviews, Series B 71, 21R-31R.
- Nee, S., May, R.M., 1992. Dynamics of metapopulations—habitat destruction and competitive coexistence. Journal of Animal Ecology 61, 37–40.
- Nonaka, E., Holme, P., 2007. Agent-based model approach to optimal foraging in heterogeneous landscapes: effects of patch clumpiness. Ecography 30, 777–788. Ottaviani, D., Cairns, S.C., Oliverio, M., 2006. Body mass as a predictive variable of home-
- range size among Italian mammals and birds. Journal of Zoology 269, 317–330.
- Pita, R., Mira, A., Beja, P., 2010. Spatial segregation of two vole species (*Arvicola sapidus* and Microtus cabrerae) within habitat patches in a highly fragmented farmland landscape. European Journal of Wildlife Research 56, 651–662.
- Prugh, L.R., Hodges, K.E., Sinclair, A.R.E., Brashares, J.S., 2008. Effect of habitat area and isolation on fragmented animal populations. Proceedings of the National Academy of Sciences of the United States of America 105, 20770–20775.
- R Development Core Team, 2008. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. (http:// www.R-project.org).
- Ritchie, M.E., 1998. Scale-dependent foraging and patch choice in fractal environments. Evolutionary Ecology 12, 309–330.
- Rohwer, S., Ricklefs, R.E., Rohwer, V.G., Copple, M.M., 2009. Allometry of the duration of flight feather molt in birds. PLoS Biology 7.
- Said, S., Servanty, S., 2005. The influence of landscape structure on female roe deer home-range size. Landscape Ecology 20, 1003–1012.
- Said, S., Gaillard, J.M., Widmer, O., Debias, F., Bourgoin, G., Delorme, D., Roux, C., 2009. What shapes intra-specific variation in home range size? A case study of female roe deer. Oikos 118, 1299–1306.
- Saupe, D., 1988. Algorithms for random fractals. In: Petigen, H.O.S.D. (Ed.), The Science of Fractal Images. Springer, New York, pp. 71–113.
- Selonen, V., Hanski, I.K., Stevens, P.C., 2001. Space use of the Siberian flying squirrel Pteromys volans in fragmented forest landscapes. Ecography 24, 588–600.
- Skorka, P., Lenda, M., Martyka, R., Tworek, S., 2009. The use of metapopulation and optimal foraging theories to predict movement and foraging decisions of mobile animals in heterogeneous landscapes. Landscape Ecology 24, 599–609.
- Smith, A.C., Fahrig, L., Francis, C.M., 2011. Landscape size affects the relative importance of habitat amount, habitat fragmentation, and matrix quality on forest birds. Ecography 34, 103–113.
- Sutherland, G.D., Harestad, A.S., Price, K., Lertzman, K.P., 2000. Scaling of natal dispersal distances in terrestrial birds and mammals. Conservation Ecology 4 (16) (http:// www.consecol.org/vol4/iss1/art16).
- Swift, T.L., Hannon, S.J., 2010. Critical thresholds associated with habitat loss: a review of the concepts, evidence, and applications. Biological Reviews 85, 35–53.
- Swihart, R.K., Slade, N.A., Bergstrom, B.J., 1988. Relating body size to the rate of home range use in mammals. Ecology 69, 393–399.
- Thompson, P., Fox, B.J., 1993. Asymmetric competition in Australian heathland rodents: a reciprocal removal experiment demonstrating the influence of size-class structure. Oikos 67, 264–278.
- Trzcinski, M.K., Fahrig, L., Merriam, G., 1999. Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. Ecological Applications 9, 586–593.
- Van Moorter, M., Visscher, D., Benhamou, S., Börger, L., Boyce, M.S., Gaillard, J.-M., 2009. Memory keeps you at home: a mechanistic model for home range emergence. Oikos 118, 641–652.
- White, E.P., Ernest, S.K.M., Kerkhoff, A.J., Enquist, B.J., 2007. Relationships between body size and abundance in ecology. Trends in Ecology & Evolution 22, 323–330.
- Whittaker, R.H., 1975. Communities and Ecosystems. Macmillan, London. Wilcox, B.A., Murphy, D.D., 1985. Conservation strategy—the effects of fragmentation on extinction. American Naturalist 125, 879–887.
- Wissel, C., Stephan, T., Zaschke, S., 1994. Modelling extinction and survival of small populations. In: Remmert, H. (Ed.), Minimum Viable Populations. Springer, Heidelberg, Germany, pp. 67–103.