Using mass scaling of movement cost and resource encounter rate to predict animal body size—Population density relationships

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ABSTRACT

The negative relationship between body mass and population abundance was documented decades ago and forms one of the most fundamental scaling-laws in ecology. However, current theory fails to capture observed variations and the subject continues to raise controversy. Here we unify empirically observed size–abundance relationships with theory, by incorporating allometries in resource encounter rate and metabolic costs of movements. Fractal geometry is used to quantify the underlying resource distributions. Our model predicts that in environments packed with resources, body mass to population abundance relationship is less negative than the commonly assumed $-\frac{3}{4}$ power law. When resources are more patchily distributed, we predict a more negative exponent. These predictions are consistent with empirical observations. The current research provides an important step towards synthesizing metabolism, resource distribution and the global scaling of animal abundance, explaining why size–abundance relationships vary among feeding guilds and ecosystems.

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1. Introduction

We are currently facing what might be the sixth mass extinction of species (Barnosky et al., 2011), with anthropogenic habitat fragmentation and deterioration identified among the main drivers of the process (Fischer and Lindenmayer, 2007). Understanding how landscape characteristics influence composition of animal communities is thus important in order to predict and mitigate future challenges in biodiversity conservation. Many studies have focused on how individual species relate to changes in landscape structures, analyzed data from case studies of community changes in response to habitat fragmentation, or applied meta-population theory to study the effects of disconnection of habitat patches (Hanski, 1998). However, it is poorly understood how changes in landscape structures and resource distribution relate to general patterns in the community structure, such as the relationship between the mean body size (usually defined by the body mass) of individuals and population density (White et al., 2007). This is known as a size–density relationship (SDR).

SDR stands at the center of macroecology, and has been one of the great generalizations in ecology. Early research found that population densities of mammals tended to scale negatively with the body mass of the individuals with an exponent of $-\frac{3}{4}$, (Damuth, 1981), and the relationship was later termed the Energy Equivalence Rule (EER) (Nee et al., 1991). In a log–log plot with log(body mass) on the abscissa and log(population density) on the ordinate axis, the EER will produce a linear relationship with slope $-\frac{3}{4}$. In effect, the EER implies that within functional groups of species, species with larger body sizes tend to be present at lower densities, but the total energy consumption by a population is independent of the mean body mass of the individuals (Ernest et al., 2003). The interpretation of the relationship is that the individual energy use, in the form of basal metabolic rate ($B$), is generally expressed as $B = c_0 M^b$ where $c_0$ is a prefactor and $b$ is the body mass ($M$) to the basal metabolic rate scaling exponent. The EER is thus an empirical realization of the basic equation $N \propto \frac{R}{b} \propto \frac{R}{c_0 M^b} \propto M^{-b}$, where $R$ is the amount of available resources and $N$ is the population abundance. While controversy exists over the mechanisms creating such a pattern (see e.g. Polishchuk and Tsetitlin, 1999), it does remind us that population abundances will ultimately be limited by the metabolic costs of animals and the availability of finite energy resources. The importance of energy supply for population abundances is also supported by the fact that consumer populations frequently scale positively with resource densities (Pettorelli et al., 2009).

The EER is tempting as a simple generalization of a central ecological pattern, and has received attention also during the last decade (Dobson et al., 2003; Ernest et al., 2003; Hayward...
et al., 2010). However, results from empirical studies (Blackburn et al., 1993; Nee et al., 1991) and predictions from theoretical models (Carbone et al., 2007) suggest that the SDR depends on the system under study. In a recent review of empirically estimated SDRs, Isaac et al. (2011) found a large variation in the reported scaling exponents. Accordingly, EER should only be expected under certain combinations of resource distributions and productivities (Carbone et al., 2007), and might be an exception rather than a rule (Isaac et al., 2011; DeLong, 2011). The inherent size scaling relationships between consumers and their resource distributions must be expected to affect SDRs (Ritchie, 2009), and previous theoretical work has indeed suggested that the underlying resource distribution might be important to understand variation in SDRs (Carbone et al., 2007).

Here, we develop a model that explicitly incorporates resource distribution in the landscape and predicts relationships between average body mass of the individuals and population densities. Our model builds on a previously published model that used a fractal description of the resource distribution in the landscape (Halley et al., 2004; Mandelbrot, 1983) and mass-scaling relationships (Ritchie, 2009). The framework is structured around a model presented by Haskell et al. (2002), which was developed to describe body mass scaling of home range sizes. Through our model we show how important and biologically sound modifications of this framework result in a model that still contains a limited number of parameters, but is more realistic and better able to predict the observed variation in SDRs. Following Carbone et al. (2007), many of these mechanisms will themselves be related to body mass following power laws. Finally, we test our model’s predictions against empirical data based on literature values of SDRs, and give a short presentation of its application. At this stage, our model does not consider top–down effects or interspecific competition, but the relatively simple model structure allows for their incorporation at a later stage.

2. General modeling framework

The term “fractal” is used to describe any geometric form that has some degree of self-similarity (Mandelbrot, 1983). Fractals are self-similar because at every spatial scale, the larger shape is composed of smaller and smaller versions of the exact same shape. Fractal patterns (Halley et al., 2004; Mandelbrot, 1983) are increasingly used to describe and quantify spatial patterns in ecological studies, e.g. to quantify structure and resource distributions in landscapes (Halley et al., 2004), model variation in bird and mammalian home range sizes (Haskell et al., 2002), and predict size frequencies of invertebrates (Kostylev et al., 2005; Morse et al., 1985). Here, we adopted the mass-fractal dimensions approach, where total amount of resources encountered (R) by individuals searching for resources in a fractal landscape is modeled as a function of the length of the sides of the search window (w) covered in a given time unit (t) (Fig. 1(a)), and the parameters c₁ and F describe the resource distribution; R = c₁w^F (see e.g. Haskell et al., 2002; Olff and Ritchie, 2002). The constant c₁ represents both the resource density and the amount of clumping (i.e. lacunarity), F describes the fractal dimensions or the degree at which resources fill space (e.g. habitat fragmentation) (Olff and Ritchie, 2002), and w is the side length of the search window, being a quadratic in two-dimensional habitats and a cube in three-dimensional habitats. F can range from 0 (resources being located in a single point), to 3 (describing resources filling a cube, see Haskell et al., 2002). F cannot exceed the dimensions of the habitat; thus F ≤ D, with D being 2 or 3 for two- and three-dimensional habitats, respectively.

Assuming a random movement trajectory and no relationship between body mass and sampling volume (i.e. the area or volume covered per unit of distance moved), the model developed by Haskell et al. (2002) expressed resource density as c₁w^F = c₁w^D. The sides of the search window are related to body mass so that w ∝ c₁M^q, where q is the size scaling of distance moved per time unit and c₁ is a constant. Across taxa the size scaling of locomotive ability q has been reported in the range between 0.16 and 0.33 (Bejan and Marden, 2006; Schmidt-Nielsen, 1984). The above arguments suggest that the scaling between body mass and abundance is ∝ c₁(c₁M^q)^F c₁M^q(F M^p). Haskell et al.’s (2002) model, originally developed to predict the scaling of home-range sizes, can therefore be rearranged and simplified in order to describe SDR:

\[ N \propto M^{-b+q(F-D)} \]  

In a landscape where resources do not completely fill the available space (i.e. F < D), increasing w would result in a lower resource density, suggesting SDRs that are always more negative than −b (except when F = D and the scaling equals −b) (Fig. 1(b)). The fact that empirical studies commonly report SDRs that are less negative than −b (e.g. Isaac et al., 2011; Hayward et al., 2010) suggests that this model does not adequately capture the empirically observed SDRs.

3. Incorporating directed walks, body mass dependent movement costs and perception ranges

In the following we describe how incorporating important and biologically sound modifications into the above described model leads to the genesis of a model that better describe observed variation in SDRs.

3.1. Cost of movement

The energetic cost of moving one unit of mass one unit of distance typically scales with body mass less steeply than b (Garland, 1983; Schmidt-Nielsen, 1984); thus moving a unit distance is not equally expensive in terms of extra energy used for movement for large and small species. The proportional increase in metabolism with movement equals c₂M^p/c₀M^p, where c₂M^p is the total metabolic cost of moving a given distance. This results in the multiplier c₂M^r setting the additional cost of moving across the landscape, where r = b₂ − b and c₁ = c₁/c₀. The scaling coefficient of the multiplier r is equivalent to the difference between the mass scaling of activity and the standard metabolism, and typically ranges between −0.07 and 0.00 (Garland, 1983; Schmidt-Nielsen, 1972, 1984).

\[ N \propto M^{-b+r+q(F-D)} \]  

Given the suggested literature values for r (−0.07 to 0.00), this should have a minor influence on the SDRs on its own, but is retained in the model because it is important for further model development.

3.2. Directed vs random movements

Theoretical and empirical studies suggest that animals do not move across the landscape harvesting resources at random but integrate prior information of habitat structure into their search pattern, and hence adopt search patterns that reduce the actual distance moved to cover a search window (e.g. a day- or home range) (see e.g. Etzehouse et al., 1998; Papastamatiou et al., 2011; Valeix et al., 2010). In general, random walks might be expected only when the location of resources is unknown and more directed walks should be expected when the resource distribution is known or can be anticipated. Often, movement trajectories change between directed movements (towards a known goal)
between patches of resources and various forms of correlated random walks inside food patches where food is abundant (see e.g. Fig. 2 in Doerr and Doerr, 2004; Papastamatiou et al., 2011). Measured by the movement path, the realized dimension of the habitat ($D'$) will therefore be smaller than the actual dimensionality ($D$) (Papastamatiou et al., 2011; Ritchie, 1998), and can range between 1 (a straight line between food patches) and $D$ (a complete random movement path). Consequently, if individuals are not moving at random, resource density in the landscape (also representing the resource encounter rate) does not relate to $w$ as $c_1 w^{D-D'}$. Rather, the resource density obtained per unit distance moved (i.e. resource encounter rate) in a given landscape will scale according to $c_1 w^{D-D'}$. If we assume that an animal has perfect knowledge of the habitat and attains a search pattern to optimize the foraging efficiency (Ritchie, 1998), the movement path between resource patches will be minimized and the realized dimension of the habitat $D'$ approaches $\{F \text{ when } F > 1 \text{ or } 1 \text{ when } F \leq 1 \}$.

Inserting the above described processes into Eq. (2), we get the following equation as a basis for size-density relationships: $N \propto \frac{c_1 (c_1 M_p r)}{c_0 M_p c_0 M_p (c_1 M_p r)^p}$. Rearranging the equation, we get:

$$N \propto M^{b+c(F-D')} = M^{b+c(F-D')}.$$  (3)

Incorporating directed movements into Eq. (3) results in a model that predicts SDRs close to $-(b+r)$ for habitats where $F > 1$, and more negative slopes in landscapes where the resources are more fragmented (Fig. 1(c)).

3.3. Body mass scaling of sensory perception range

The area or volume sampled for resources per unit distance moved (sampling volume) is not independent of body mass, and depends on the scaling of e.g. the sensory acuity (Kiltie, 2000) or capture range of the consumer. The effect of such a process is that, for a given fractal resource distribution, encounter rates increase with body mass. Writing $p$ for the body mass scaling of the sensory perception range, movement distance needed to
sample the resources in a search window with sides \( w \) does not scale according to \( w \propto (M^D)^1 \), but rather as \( \frac{M^D}{M^P} = (M^D)^{D-P} \). Inserting the above described processes into Eq. (3), we propose the following equation as a basis for SDRs: 
\[
N \propto \frac{M_{1}^{c_{1}c_{3}M^{F}}}{C_{0}M^{P}C_{2}M^{q}D^{D-P}}.
\]
Rearranging the equation, we get:
\[
N \propto M^{-b+q(F-(D'-p))-1} = M^{-b-r+q(F-(D'-p))}. \tag{4}
\]
Values for \( p \) integrating both sensory range and capture range are hard to obtain, but \( p \) must be expected to be substantially larger than zero (Goldbogen et al., 2010; Kiltie, 2000). A few available studies have reported relationships close to isometric (Goldbogen et al., 2010; Kiltie, 2000), and we use this value here to incorporate the effect of sensory range scaling on SDR. It is quite clear, however, that further studies are needed to understand the body mass scaling of \( p \). As \( p \) in effect increases the resource encounter rate per unit distance traveled and thereby the amount of resources encountered along a movement path, it is related to the dimensions of the movement path represented by the realized dimensionality of the landscape \( D' \). If \( D' = 1 \), all resources are found as points on a straight line and \( p \) does not affect the movement path, ensuring that all available resources within a search volume are encountered. If \( D' = 2 \) (e.g. a filled quadrate), this assumption implies that the encounter rate along a movement path is doubled when the body mass is doubled, as suggested by the \( M^1 \) scaling. If \( D' = 3 \) (a filled cube) with resources distributed along three axes, the sampling volume along a movement path is cubed when body mass is doubled. When incorporating variation in \( D' \) into the scaling of sampling volume, \( p \) becomes \( \approx D' - 1 \). The SDR then simplifies to:
\[
M^{-b-r+q(F-1)}. \tag{5}
\]

4. Model predictions and fit to empirical data

In our final model (Eq. (5)) the number of dimensions \( (D) \) does not enter the equation, except by setting the maximal value for \( F \) (i.e. \( F \leq D \)). Based on this model, we predict SDRs that are dependent on the relationship between the scaling factors \( q \) (movement speed) and \( r \) (movement costs), and the fractal dimensions of the landscape \( F \). Since search volume scales positively with body mass \( (q > 0) \) and additional costs of movement negatively \( (r < 0) \) (Bejan and Marden, 2006; Garland, 1983; Schmidt-Nielsen, 1984), SDRs will be more negative than \( -b \) when \( q(F-1) < r \), and less negative when \( q(F-1) > r \). Assuming that \( r \) and \( q \) does not vary dramatically among systems, the model importantly predicts a more negative SDR with decreasing fractal dimensions, corresponding to a situation with a more fragmented resource distribution. Indeed, given the range of reported values of \( q \) and \( r \), the variation in \( F \) will largely drive the variation in the SDR (Fig. 1(d)). The predicted SDR decrease with decreasing \( F \) values from \(-0.05\) to \(-1.1\). For \( F \) values greater than 1 the model predicts SDRs shallower than \(-b\). With mass scaling of movement costs similar to \( b \) \((r = 0)\) and no relationship between body mass and search windows \((q = 0)\), we get the conventional \(-b \) scaling between abundance and body mass, independent of landscape structure. This is equivalent to the situation with sessile animals or plants, which indeed tend to have more consistent patterns of SDRs, being close to \(-b \) (Brown and West, 2000; Enquist and Niklas, 2001).

As an initial empirical confrontation of our model (Eq. (5)), we used feeding guild as a proxy for the fractal resource distribution as their feeding habitats will frequently be described by different \( F \) values (see also Haskell et al., 2002). The habitat dimension \( (D) \), setting the upper limit for \( F \), was approximated by classifying species belonging to the pelagic or forest–canopy habitats, as well as all birds except typically ground-dwelling ones, as inhabiting three-dimensional habitats (see appendix). All other species where classified as inhabiting two dimensional habitats. Although this approach constitutes a simplification of the true dimensionality of natural habitats, it serves as a useful proxy for our conceptual comparison. We fairly acknowledge that this empirical test is preliminary and that the fact that predictions from a general model fit some overall patterns in the data does not imply that the proposed mechanisms need to be correct. Note also that our data set will include a variation in data types (i.e. “individual
size relationships”, “global size–density relationships” and “local size–density relationships”; sensu White et al., 2007), and thus might be somewhat confounded by the different mechanisms that affects size–abundance relationships (White et al., 2007). The majority of the studies in our database are based on “global size–density relationship” type of data, as originally plotted by Damuth (1981).

In general, fractal dimensions of resource distributions will decline with increasing trophic level (Haskell et al., 2002), partly because the amount of resources will decrease upwards in the food web, yielding a larger food base for primary consumers (Ricklefs, 1996). In our analyses, we only included data sources that unambiguously identified either feeding guild or species names, so that food resource and feeding habitat could be identified (n = 106; details and references in Table S1, Appendix, Online supporting information). Our model correctly predicts the systematic trend in SDRs between feeding guilds experiencing different resource distributions (Fig. 2(a)). Mean observed SDRs varied from −0.54 (±0.05 SE), −0.76 (±0.21 SE) to −1.04 (±0.10 SE) for herbivores, invertebrate feeders and predatory species, respectively (ANOVA: F_{2,102} = 5.85, p = 0.004). In addition, for communities inhabiting three-dimensional habitats, the maximum value for F is higher than for communities inhabiting two-dimensional habitats. All else being equal at the maximum potential value for F, our model predicts shallower slopes for herbivores in three-dimensional habitats compared to two-dimensional habitats (Fig. 2(b)). This prediction fits well the observed patterns in the data, with communities inhabiting three-dimensional habitats having on average less negative SDRs (−0.06 ± 0.08 SE) than herbivores inhabiting two-dimensional habitats (−0.62 ± 0.05 SE) (t-test, df = 66, p < 0.001).

5. Discussion

In this paper we have presented a model developed from first principles that incorporates resource distribution in the landscape and important biological sound mechanisms describing how animals move around in the landscape harvesting resources. Based on this model, we predict how size–density relationships (SDR) are affected by the resource distribution in the landscape. Our model predicts that in environments packed with resources, body mass to population abundance relationships are less negative than the commonly assumed −3/4 power law. When resources are more patchily distributed, we predict a more negative exponent. In general, these predictions are consistent with empirical observations.

A range of factors affects the dynamics and abundance of animal populations (Nilsen et al., 2009), and no single model derived from first principles is likely to correctly predict animal abundances in a given community. We would stress that our model assumes that populations are limited by the amount of resources and does not consider how trophic interactions such as competition and predation structure ecological communities (Loeuille and Loreau, 2006; Rossberg et al., 2008). Hence, when studying SRDs in a single local community, factors other than resource limitation might prevail, causing variation in reported SDR-scaling. However, our model predictions fit well with the general patterns of variation in SDR-scaling that are related to the resource distributions and the costs involved when moving in the landscape harvesting resources. Complying with recent empirical findings (Carbone et al., 2010) and theoretical work (Carbone et al., 2007), our bottom–up model predicts that larger species should be favored under high resource densities and smaller species under low resource densities. This prediction could contribute to a better understanding of extinction processes both in present and prehistoric times. In landscapes experiencing increased anthropogenic land use and changing habitat patterns, habitat loss and fragmentation have been shown to have separate effects on biodiversity (Fahrig, 2003; Olff and Ritchie, 2002). According to our model, large-bodied species will be expected to be more sensitive than small-bodied species to these effects, as their abundances will be relatively more affected. Noting that gigantic dinosaurs such as the sauropods thrived in the prehistoric world with abundant resources (McNab, 2009), our bottom–up model would predict that, all else being equal, such large bodied species would have been hit particularly hard when environmental change resulted in resources becoming fragmented and sparse. Following the above discussion, we will not claim here that we have developed a definitive model for mass-abundance scaling in animal communities. However, as a null model for studying body size–population density relationships, we suggest that no single scaling between body size and abundance is expected to occur across systems, and that our model might provide a mechanistic bridge to empirical observations.
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Appendix. Supplementary data

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