

LETTER

Evolution of body size in food webs: does the energetic equivalence rule hold?

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Abstract

The energetic equivalence rule (EER), which is derived from empirical observations linking population density and body size and from the allometric law linking metabolism and body size, predicts that the amount of energy used by the various species should be independent of body size. Here, we examine this hypothesis using a model that allows entire food webs to emerge from coevolution of interacting species. Body size influences both individual metabolism and interactions among species in the model. Overall, population density does decrease with body size roughly following a power law whose exponent is variable. We discuss this variability in the light of empirical data sets. The emerging relationship between the flux of resources exploited by the various species and their body size follows a decreasing power law, thus contradicting the EER. Our model emphasizes the importance of considering the influence of body size on species interactions in attempting to explain large-scale patterns related to body size.

Keywords

Adaptive dynamics, body size, coevolution, energetic equivalence rule, trophic structure.

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INTRODUCTION

Body size is one of the most conspicuous traits of the various species present on Earth; it is also one of the easiest traits to measure. As a consequence, numerous studies are concerned with body size and how it may be linked to other characteristics of organisms and their populations (Peters 1983). At the individual scale, body size influences metabolic rate (Hemmingsen 1960; Kleiber 1961), and hence also growth rate and mortality rate (Peters 1983). Body size may also be related to various life-history traits, such as survivorship, clutch size, egg mass, breeding time, life span and dietary niche in birds (Blackburn *et al.* 1996; Brändle *et al.* 2002), and to other physiological traits as diverse as locomotion, respiration, ingestion and physiology for many kinds of organisms (Peters 1983).

At the population and community scale, body size appears to be linked to parameters such as population density (Sheldon *et al.* 1972; Damuth 1981, 1991, 1993; Peters 1983; Brown & Maurer 1986, 1989; Marquet *et al.* 1990, 1995; Nee *et al.* 1991; Greenwood *et al.* 1996; Enquist *et al.* 1998; Cohen *et al.* 2003; Russo *et al.* 2003), habitat range (Brändle *et al.* 2000), species frequency (Brown & Maurer 1989; Brown *et al.* 1993; Greenwood *et al.* 1996; Boback & Guyer 2003) and total production (Sheldon *et al.*

1973; Enquist *et al.* 1999; Jennings *et al.* 2002a). The links between body size and species frequency or population density have been particularly debated during the past decades. Part of the debate was obscured by the differences in the nature of the data under study. For example, some studies focused only on certain groups of animals (birds: Nee *et al.* 1991; Blackburn *et al.* 1996; Russo *et al.* 2003, mammals: Damuth 1981, 1993; Aava 2001, birds and mammals: Greenwood *et al.* 1996, snakes: Boback & Guyer 2003) or plants (Enquist *et al.* 1998), while others mixed all kinds of organisms together (Marquet *et al.* 1990; Cohen *et al.* 2003). Some considered a community at a given location (Marquet *et al.* 1990; Aava 2001; Cohen *et al.* 2003; Russo *et al.* 2003), while some others compiled data coming from different communities (Damuth 1981, 1991, 1993; Nee *et al.* 1991; Blackburn *et al.* 1996; Greenwood *et al.* 1996; Boback & Guyer 2003).

Some studies support the view that density D and body mass x are linked by a power law $D \propto x^b$ (Damuth 1981, 1991, 1993; Marquet *et al.* 1990; Nee *et al.* 1991; Greenwood *et al.* 1996; Enquist *et al.* 1998; Cohen *et al.* 2003; Russo *et al.* 2003). The value of the exponent b is very often close to -0.75 (Damuth 1981, 1991, 1993; Marquet *et al.* 1990; Nee *et al.* 1991), a commonly found value in allometry (Peters 1983).

The energetic equivalence rule (EER) (Damuth 1981; Nee *et al.* 1991) claims that the amount of energy E consumed by a given species is independent of its body size, for the following reasons:

- (1) the empirical data sets used by Damuth (1981) show that the relationship between density D and body size x is roughly $D \propto x^{-0.75}$;
- (2) metabolism B is assumed to be linked to body size by the power law $B \propto x^{0.75}$.

As a result, energy use E , which is supposed to be the product of density and metabolism: $E \propto DB \propto x^{-0.75} x^{0.75} \propto x^0$, should be independent of body size.

Criticisms of the EER may be divided in three categories:

- (1) criticisms of the empirical observation $D \propto x^{-0.75}$ by the study of other empirical data sets: the exponent was found to be significantly different from -0.75 in a number of cases (Cohen *et al.* 2003; Russo *et al.* 2003) or to be highly variable (Brown & Maurer 1986; Greenwood *et al.* 1996);
- (2) criticism of the methodology (fallacy of the averages: Medel *et al.* 1995);
- (3) criticism of its theoretical grounds (Marquet *et al.* 1995).

Although the EER is sometimes regarded as an empirical pattern, we wish to stress here that we regard it as a hypothesis. For the EER to be an empirical pattern, it should be based on empirical data sets showing that energy consumption is independent of body mass in ecosystems. While there are many data sets about the relationship between population density and mean body mass, data sets that relate energy consumption to body mass are scarce and do not provide a strong empirical support for the EER. For this reason, we consider the EER as a hypothesis that is derived from empirical observations on density–body mass relationships, but which also contains a number of

underlying assumptions. These assumptions should be examined carefully from a theoretical perspective, which we attempt to do in this paper.

Damuth (1981) speculated that the EER may emerge from macroevolution of coevolving, interacting species (see also Maiorana & Van Valen 1990; Marquet *et al.* 1995). The model presented here allows entire food webs to emerge from coevolution of interacting species. Our model assumes that body size is the trait under selection that determines trophic and competitive interactions among species, as well as metabolism according to the power laws discussed above. This coevolutionary model is particularly adapted to examining the theoretical basis of the EER because it involves a macroevolutionary assembly of a community based on body size constraints acting at the individual level. It incorporates the relationship between metabolism and body size that is the cornerstone of the EER, but it also takes into account the fact that body size affects ecological interactions. The relationships between population density, energy use and body size emerge as higher-level properties of these individual-level constraints. We mainly focus on two questions in the interpretation of the results

- (1) What kind of relationship between population density and body size emerges from our model and what is its relevance to empirical data sets?
- (2) What kind of relationship between energy use and body size emerges from our model, and what are its implications for the EER?

Presentation of the model

The model we use here is identical to the model presented in Loeuille & Loreau (2005). Equations are recalled in Table 1, and parameters are recapitulated in Table 2. In this model,

Table 1 Equation of the model

Description	Equation
Dynamics of a species N_i with size x_i	$\frac{dN_i}{dt} = N_i \left(f(x_i) \sum_{j=0}^{i-1} \gamma(x_i - x_j) N_j - m(x_i) - \sum_{j=1}^n \alpha(x_i - x_j) N_j - \sum_{j=i+1}^n \gamma(x_j - x_i) N_j \right)$
Dynamics of inorganic nutrient $N_0(x_0 = 0)$	$\begin{aligned} \frac{dN_0}{dt} = & I - eN_0 - \sum_{i=1}^n \gamma(x_i) N_i N_0 \\ & + v \left(\sum_{i=1}^n m(x_i) N_i + \sum_{i=1}^n \sum_{j=1}^n \alpha(x_i - x_j) N_i N_j \right. \\ & \left. + \sum_{i=1}^n \sum_{j=1}^n (1 - f(x_i)) \gamma(x_i - x_j) N_i N_j \right) \end{aligned}$
Production efficiency	$f(x) = f_0 x^{-0.25}$
Mortality rate	$m = m_0 x^{-0.25}$
Rate of interference competition between species i and j	$\alpha(x_i - x_j) = \begin{cases} \alpha_0 & \text{if } x_i - x_j < \beta \\ 0 & \text{else} \end{cases}$
Rate of predation exerted by species i on the smaller-sized species j	$\gamma(x_i - x_j) = \frac{\gamma_0}{s\sqrt{2\pi}} \exp\left(\frac{-(x_i - x_j - d)^2}{s^2}\right) \quad (x_i > x_j)$

Table 2 Variables and parameters of the model

	Unit	Description
Variable		
N_i	kg	Nutrient stock of species i
x_i	kg	Body size of species i
Parameter		
I	kg s ⁻¹	Inorganic nutrient input
e	s ⁻¹	Rate of inorganic nutrient loss
v	dimensionless	Fraction of nutrient recycled within the system
m_0	s ⁻¹	Mortality rate for a species with unit body size
f_0	dimensionless	Production efficiency (conversion of resources into new offspring) of a species with unit body size
α_0	kg ⁻¹ s ⁻¹	Rate of interference competition between similar-sized species
β	kg	Threshold body-size difference between species under which interference competition occurs
γ_0	s ⁻¹	Basal rate of consumption
s^2	kg ²	Variance of the size-dependent predation function
d	kg	Distance between the body size of a predator and that of its preferred prey
$nw = s^2/d$	kg	Niche width

the entire community emerges from coevolution of species given a chosen shape for the consumption niche and a chosen intensity of interference competition among similar-sized species.

The role of body size x in this model is present at several levels. First, it influences the individual growth rate through the production efficiency $f(x_i)$ and the mortality rate $m(x_i)$, which are supposed to be related to the mass-specific metabolic rate, i.e. the metabolic rate per unit of mass (Peters 1983). If an individual's metabolic rate scales as $x^{0.75}$, then its mass-specific metabolic rate scales as $x^{0.75}/x = x^{-0.25}$. Here, we assume that body size x is measured by body mass; therefore,

$$f(x) = f_0 x^{-0.25} \quad \text{and} \quad m(x) = m_0 x^{-0.25}.$$

Thereby, the model accounts for one of the allometric bases of the EER.

Second, the body size of each individual has an effect on which species it can consume and by which species it is consumed and on the strength of these trophic interactions. This effect is captured in the trophic interaction function γ , whose shape defines the consumption niche of each species. To describe this niche, we use parameter 'nw', which measures niche width. We took six values of niche width in our numerical simulations ($nw = 0.5, 1, 2, 3, 4, 5$). The function γ has a Gaussian shape such that a species with body size x is able to eat species with smaller body sizes, and its preference goes to species that are not too small (body size around $x - d$) so that energy gains are optimized. The shape of this function was also suggested by Peters (1983). The dependence of prey–predator interactions on body size is largely documented, the predator being larger than the prey in almost all cases (Elton 1927; Sheldon *et al.* 1972,

1973; Warren & Lawton 1987; Cohen 1989; Cohen *et al.* 1993; Hansen *et al.* 1994; Jennings *et al.* 2002a,b, at least as long as predators are defined *sensu stricto*, for this rule does not hold for parasites (Leaper & Huxham 2002).

Third, body size determines the other species with which each species will be in interference competition (Bowers & Brown 1982). Indeed, if two species have sizes that are similar enough (their size difference is below a threshold value β), they are supposed to interfere physically (Rosenzweig & Sterner 1970; Hafner 1977). A possible mechanism of competition may be the link between size and habitat partitioning (Price 1978). In the case of the present model, the threshold size difference β is very low, and thus interference competition occurs mainly with individuals of the same species or with nearby mutants. We took six values for competition intensity in our simulations ($\alpha_0 = 0, 0.1, 0.2, 0.3, 0.4, 0.5$), including 0, which corresponds to the case where interference competition does not occur. However, communities arising from the simulations without interference competition have low species diversity (Loeuille & Loreau 2005). The combination of parameters ($nw = 5, \alpha_0 = 0$) even leads to an evolutionary suicide, species diversity then being zero.

Evolution within each community was simulated starting with a single species consuming inorganic nutrient. The dynamics of food web assembly contains two components that occur simultaneously: population growth and mutations. The equations of population dynamics (Table 1) are simulated using the Runge–Kutta method. At each time step, after computing the new population sizes, mutations may happen. Mutants that differ slightly in body size appear with a probability of 10^{-6} per unit of mass and unit of time. Their initial population size corresponds to the extinction

threshold below which a species goes extinct. Population dynamics then selects or counterselects the mutation. During the course of evolution, an evolutionary branching may occur, leading to a second species coexisting with the first. As other evolutionary branchings occur, a food web appears gradually, whose emergent properties (presence of distinct trophic levels or not, proportion of omnivores, total biomass, species diversity, nutrient recycling, etc., see Loeuille & Loreau 2005), may differ greatly depending on niche width nw and competition intensity α_0 .

The population density of each species i is computed simply as its nutrient stock N_i divided by its body mass x_i . The results presented here correspond to communities that are at an evolutionary quasi-equilibrium, i.e. mutants able to invade the community are very rare, and when they arise, they usually replace a species with a similar trait, such that the overall community-wide patterns remain roughly constant. This was true for all the simulations presented. These were run for 10^8 time steps, which proved sufficient to attain a quasi-equilibrium state (Loeuille & Loreau 2005).

RESULTS

Figure 1 shows the relationship between population density and body size for four sets of parameters ($\alpha_0 = 0.1$ or 0.2 and $nw = 0.5$ or 5). Curves (a) and (c), which correspond to narrow niches ($nw = 0.5$) approximately match a power law between population density and body size, $D \propto x^b$. Curves (b) and (d), which correspond to broad niches ($nw = 5$), differ slightly from a power law. Large species are less abundant than expected from the power law and there are

few species that have a small body size and a large density. Variability around the general trend is also noteworthy. When niche width is low [$nw = 0.5$, panels (a) and (c)], the overall power law results from the juxtaposition of three distinct groups of points. In this case the food web is structured in well distinct trophic levels (Loeuille & Loreau 2005). The three groups of points correspond to different trophic levels. Within each group, the middle points are higher, which means that within each trophic level, there is a maximum of population density for an intermediate body size. Thus, our results support the hypothesis that within a guild, population density is maximum at an intermediate body size (Gaston 1988; Gaston & Lawton 1988; Morse *et al.* 1988; Brown & Maurer 1989, but see Currie 1993), even though the power law $D \propto x^b$ holds when all guilds are considered. On the contrary, when nw is large [$nw = 5$ as in panels (b) and (d)], population density gradually decreases with body size. This case corresponds to communities in which trophic levels cannot be easily distinguished (Loeuille & Loreau 2005). These patterns are robust to changes in competition intensity, as shown by comparison between top and bottom panels in Fig. 1.

Figure 2 shows the value of the exponent b of the power law $D \propto x^b$ as a function of the two parameters under study, i.e. niche width and competition intensity. The community corresponding to the couple of parameters ($\alpha_0 = 0$, $nw = 5$) does not exist because this situation leads to an evolutionary suicide. Other communities with no interference competition ($\alpha_0 = 0$) have only very few species. For this reason, the exponent b is very variable through time and barely significant. Consequently, we excluded these points

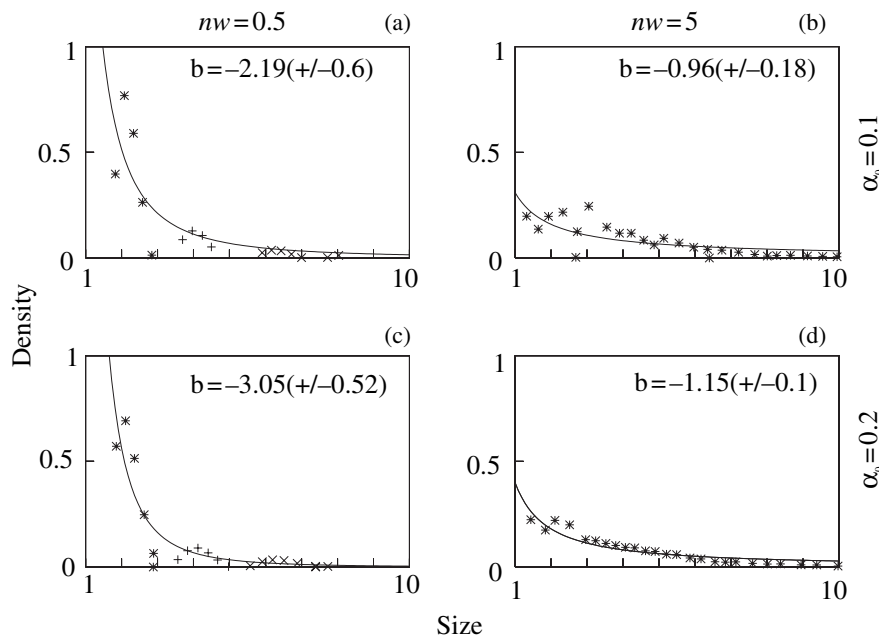


Figure 1 Relationship between population density and body size across species, for different values of niche width (nw) and competition intensity (α_0). Lines correspond to the best least-square fit of the power law $D \propto x^b$ (nonlinear regression, untransformed data). In the panels (a) and (c), food webs have distinct trophic levels that are symbolized by different types of points. Values of the exponent b are mentioned, as well as its standard deviation. Note that when niches are large ($nw = 5$), large species are less common than expected from the power law. Other parameter values: $I = 10$, $e = 0.1$, $v = 0.5$, $\gamma_0 = 1$, $d = 2$, $f_0 = 0.3$, $m_0 = 0.1$, $\beta = 0.25$).

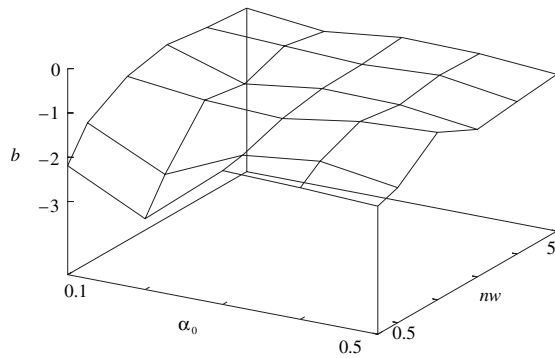


Figure 2 The exponent b of the power law $D \propto x^b$ relating population density and body size as a function of niche width (nw) and competition intensity (α_0). Parameter values as in Fig. 1.

from Figs 2, 4 and 5. Overall, the exponent b tends to decrease as nw decreases and as α_0 increases. The negative effect of competition intensity α_0 on b may be explained by a decrease in the biomass of the various species because of increasing interspecific competition. This negative effect is more important for large species at the top of the food web than for small species at the base of the food web, because increasing competition increases mortality and hence nutrient recycling. Inorganic nutrient is then more abundant, which leads to a positive indirect effect on the base of the food web. The effect of niche width nw may be explained by its effect on food-web structure. When the niche is narrow (nw is low), the food web consists of well-differentiated trophic levels. During the consumption process, only a proportion ϵ of the nutrient is transmitted from a trophic level to the next. Because of these nutrient

losses, population density decreases rapidly from the bottom to the top of the food web. Therefore, the relationship between population density and body size is steep. When the niche is large (high values of nw), trophic levels cannot be distinguished. These food webs contain a large proportion of omnivores and food chain length is reduced. This configuration limits the total amount of nutrient lost because of predation. Population density still decreases with body size, but this decrease is less steep.

We also measured the amount of resources E_i exploited by each species i , and examined how it depends on body size. For a given species i , the total amount of resources consumed corresponds to the total nutrient flux linked to the consumption process:

$$E_i = \sum_{j=0}^{i-1} \gamma(x_i - x_j) N_j N_i.$$

The relation between energy consumption and body size are plotted on Fig. 3 with the same sets of parameters as in Fig. 1. Note that the relation between the incoming flux of resources E and body size x also approximately follows a power law $E \propto x^g$, where g is different from 0. Therefore, it does not support the prediction made by the EER. As in the case of the relation between population density and body size, the exponent g of the power law strongly depends on niche width and competition intensity (Fig. 4).

Note that Figs 1 and 2 appear to be very similar to Figs 3 and 4. Although the exponents of the power laws are similar in both cases, the decrease is steeper in the case of the density–size relation than in the case of the flux–size

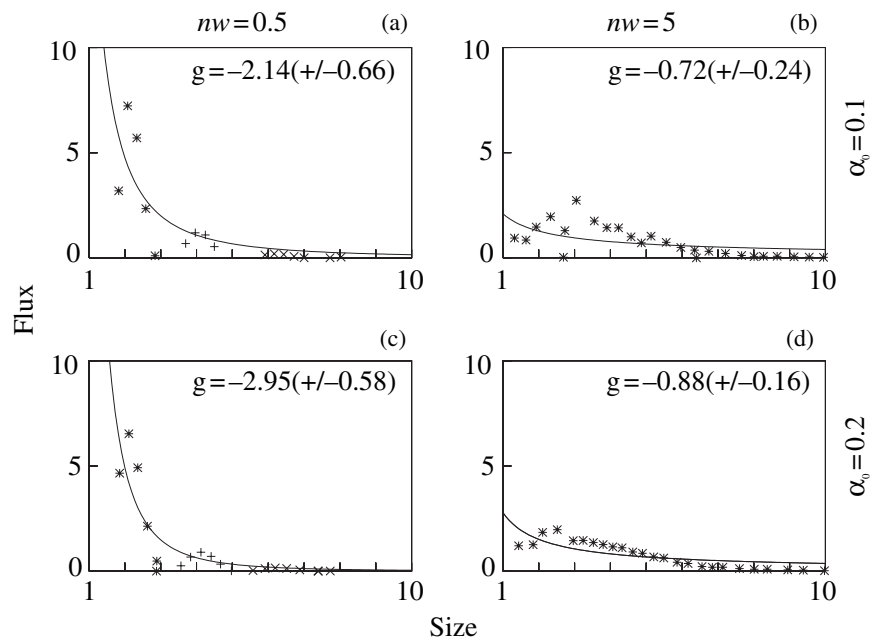


Figure 3 Relationship between the flux of resources consumed by the various species and their body size, for different values of niche width (nw) and competition intensity (α_0). Lines correspond to the best least-square fit of the power law $E \propto x^g$ (nonlinear regression, untransformed data). In the panels (a) and (c), food webs have distinct trophic levels that are symbolized by different types of points. Values of the exponent g are mentioned, as well as its standard deviation. Parameter values as in Fig. 1.

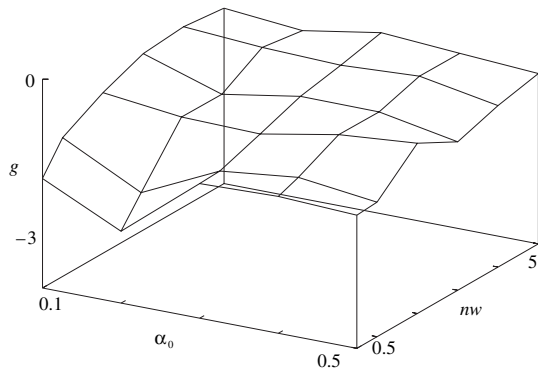


Figure 4 The exponent g of the power law $E \propto x^g$ relating resource consumption and body size as a function of niche width (nw) and competition intensity (α_0). Parameter values as in Fig. 1.

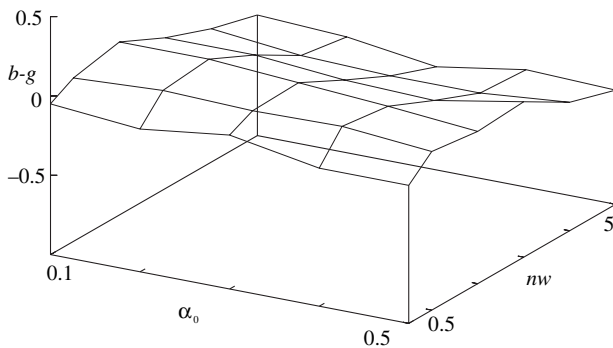


Figure 5 Difference between the exponent b of the power law relating population density and body size and the exponent g of the power law relating resource consumption and body size, as a function of niche width (nw) and competition intensity (α_0). Parameter values as in Fig. 1.

relation when nw is either large or zero, the reverse being true when nw is intermediate (see Fig. 5).

DISCUSSION

As far as we know, the present model is the first to incorporate allometric constraints related to body size, explicit population dynamics and evolution of body size at the scale of an entire community or ecosystem. As the model incorporates the effects of body size on production efficiency and mortality rate, the metabolic bases of the EER are explicitly considered here, but the model also includes the effects of body size on trophic and competitive interactions.

Taking a limiting nutrient as a currency for the present model allows a more straightforward approach to the functional aspects of the community (e.g. recycling process and quantity of resources ingested). Expressing the mutation rate per unit of biomass may be more questionable biologically, but we focus here only on the quasi-equilibrium

states of the community, and this state is determined by the fitness landscape of the community, and hence on the parameters of the model, not on the mutation process. We also assume that population density is simply the ratio between the nutrient content of a species and its body mass. This means that we assume individual body mass to be proportional to its content in the limiting nutrient, which should be approximately across wide variations of body size (but see Sterner & Elser 2002, pp. 171–175, for a discussion on the relationship between body size and N : P ratio).

The relation between population density and body size that emerges from our model very roughly follows a power law. However, the exponent of this approximate power law is very variable and may be very different from -0.75 . These observations are in accordance with many empirical observations (Brown & Maurer 1986; Greenwood *et al.* 1996; Cohen *et al.* 2003; Russo *et al.* 2003). Figure 2 shows that the exponent predicted by the model is usually around -0.75 or more negative. This steep relationship between density and body size is found in many data sets (Brown & Maurer 1986; Greenwood *et al.* 1996; Cyr 2000; Brown & Gillooly 2003; Cohen *et al.* 2003; Brown *et al.* 2004). However, very steep values emerging from the model when both nw and α_0 are low do not seem to happen in nature. Furthermore, Fig. 2 does not display exponents larger than -0.75 , although these values appear in several data sets (Brown & Maurer 1986; Russo *et al.* 2003). As noted in the Results section, the exponent b increases rapidly when niche width, nw increases. Therefore, we expect the model to be able to account for flatter density–body size relationship for larger values of the niche width parameter.

Some authors have suggested that the density–body size relationship is steeper (exponent around -1) in food webs than within trophic levels (exponent around -0.75) (Cyr 2000; Brown *et al.* 2004, Marquet *et al.* 2005). In the present model, the conditions for the emergence of distinct trophic levels (narrow niches and low competition) are also the conditions for the emergence of steep relationships between density and body size. Food webs emerging for other parameter values are reticulate and have a large proportion of omnivores, which makes trophic levels indistinguishable. In these cases, the exponent of the density–body size power law is closer to -0.75 .

An interesting feature of the model is that it is able to reconcile observations showing a maximum population density at an intermediate body size (Gaston 1988; Gaston & Lawton 1988; Morse *et al.* 1988; Brown & Maurer 1989, but see Currie 1993), and others showing a power law decrease in population density with body size (Damuth 1981, 1991, 1993; Marquet *et al.* 1990; Nee *et al.* 1991; Greenwood *et al.* 1996; Enquist *et al.* 1998; Cohen *et al.* 2003; Russo *et al.* 2003). When niches are narrow (e.g. $nw = 0.5$ in Fig. 1a,c), the overall relation between population density and body size

across the whole body-size gradient follows a power law, but one may clearly distinguish three intermediate maxima over smaller sections of the body-size gradient, one for each of the trophic levels of the community. Thus, the power law applies at the level of the entire community while the intermediate maximum density applies within each guild. The distinction between within-guild and between-guild patterns has recently been emphasized for the relationship between number of species and body size by Etienne & Olff (2004). Their model is based on neutral theory within guilds and an allometric law between guilds, and produces an intermediate maximum in the number of species when plotted against body size within guilds. In comparison, our model allows the emergence of such density maxima at intermediate body sizes and the emergence of the guilds themselves simultaneously, without imposing the hypothesis that different mechanisms should occur within and between guilds.

As shown by Fig. 4, the flux of resources exploited by a given species is not constant, but decreases with its body size roughly according to a power law. This result contradicts the EER.

The differences between our model and standard allometric theory have two explanations. The first explanation is that, as explained above the model presented here takes into account some of the bases of allometric theory by linking production efficiency transfer $f(x)$ and mortality rate $m(x)$ to mass-specific metabolism and hence body size x , but it also incorporates the influence of body size on trophic and competitive interactions via the functions $\gamma(x_i - x_j)$ and $\alpha(|x_i - x_j|)$. Contrary to the EER, the relationship between the amount of energy exploited and body mass emerges from the intrinsic dynamics of the system. It does not involve the product of two power laws as the EER does, and is therefore immune to the fallacy of averages (Medel *et al.* 1995). When Damuth (1981) suggested that the EER might emerge from the coevolution of species, he only considered metabolic constraints. However, body size is also known to affect species interactions, a feature that our model considers explicitly. Consideration of the influence of body size on interspecific interactions is the major difference between the EER and our model. Carbone & Gittleman (2002) showed that the power law linking density and body size for carnivores has -0.75 exponent, provided that the biomass of potential prey is the same for all species. They show that if the amount of resources is not the same for all species, considerable variations are to be expected. Brown & Gillooly (2003) mention that energy invariance (EER) applies to the situation when all species use a common source of energy. In the case of the present model the range and amount of potential preys depends on the species considered, because a species with body size x preferentially consumes species whose body size is around $x - d$, the abundance of which is a result of the internal dynamics of the system. Thus, the

various species do not use a common source of energy as they do not feed on the same species and the amount of resources available to them varies. Therefore, there is no reason why all species should exploit the same quantity of resources or energy. Under the assumption of our model, our results suggest that they do not. We feel that this influence of body size on species interactions has too often been ignored so far and should be considered when attempting to explain large-scale patterns related to body size.

The second explanation for the difference between our model and standard allometric theory lies in the fact that the EER, which relies on data collected in different environments, assumes a similar supply of resources in the various environments, an assumption that has already been questioned by Marquet *et al.* (1995) and Marquet (2002). In our model, the amount of basal resources is simply the stock of inorganic nutrient N_0 . This is not a parameter, but instead a variable which changes with the set of species (and therefore the set of body sizes) during the evolutionary emergence of the community (equation, Table 1). Changes in the amount of available resources are determined not only by the input I and output rate e of inorganic nutrient in the system, but also by the consumption of nutrient by the various species and the way they recycle it. Thus, the supply of resources is a dynamic feature of the model, which changes with the trait composition of the community and therefore varies in different environments.

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