Scaling of biological rates with body size as a backbone in the assembly of metacommunity biodiversity

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The dispersal–body mass association has been highlighted as a main determinant of biodiversity patterns in metacommunities. However, less attention has been devoted to other well-recognized determinants of metacommunity diversity: the scaling in density and regional richness with body size. Among active dispersers, the increase in movement with body size may enhance local richness and decrease β-diversity. Nevertheless, the reduction of population size and regional richness with body mass may determine a negative diversity–body size association. Consequently, metacommunity assembly probably emerges from a balance between the effect of these scalings. We formalize this hypothesis by relating the exponents of size-scaling rules with simulated trends in α-, β- and γ-diversity with body size. Our results highlight that the diversity–body size relationship in metacommunities may be driven by the combined effect of different scaling rules. Given their ubiquity in most terrestrial and aquatic biotas, these scaling rules may represent the basic determinants—backbone—of biodiversity, over which other mechanisms operate determining metacommunity assembly. Further studies are needed, aimed at explaining biodiversity patterns from functional relationships between biological rates and body size, as well as their association with environmental conditions and species interactions.

Introduction

Body size is a key attribute that shapes community assembly at several scales [1–4]. In a metacommunity context, body size is related to three well-recognized determinants of metacommunity diversity: dispersal ability, local density and regional species richness (figure 1*a*) [5]. Despite their recognized potential for shaping diversity, metacommunity theory has devoted more attention to the scaling in dispersal ability than to other scaling relations [5–7]. For taxa exhibiting active dispersal strategies, dispersal ability increases with body mass [6,8]. Besides, dispersal has the potential to increase local diversity and to reduce β-diversity, provided that it is not large enough to homogenize the system [9–11]. Consequently, if the positive dispersal ability–mass scaling is considered in isolation, larger sized taxa should present higher local richness and lower β-diversity, as compared to smaller sized taxa.

In addition to the positive relation between body size and dispersal, the well-reported negative scaling in population density and regional richness with taxon body mass may contribute to explain the among-taxa differences in metacommunity diversity. Local density scales negatively with the mass of individuals [2,12,13]. Consequently, larger sized taxa present lower potential numbers of
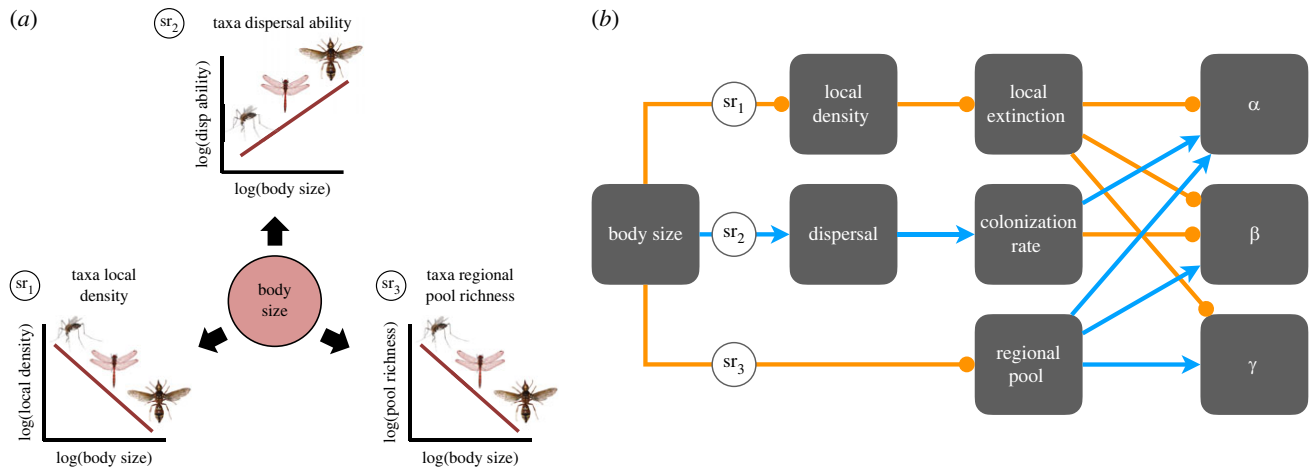
Figure 1. (a) Schematic representation showing empirical body size-scaling rules on local density (sr$_1$), dispersal ability (sr$_2$) and regional pool richness (sr$_3$). As taxa body size becomes larger, there is an increase in dispersal ability, while the richness of the regional pool and local and regional density scales negatively with taxa body size. Any of these scaling rules or their combined effects have the potential to determine metacommunity assembly and diversity patterns. (b) Theoretical chains of effects between body size and α-, β- and γ-diversity. Blue/orange arcs ending in arrows/circles represent positive/negative effects. While body size is expected to negatively affect β- and γ-diversity, there are countervailing indirect effects on α-diversity. Empirical body size-scaling rules sr$_1$, sr$_2$ and sr$_3$ are indicated.

occurring species in a community because local populations tend to be smaller and more prone to extinction, which leads to a reduction in α-diversity [2,3,14]. In addition, extinctions will disproportionately affect rare species, increasing the representation of common species across different communities, thus reducing β- and γ-diversity. Similarly, regional richness, which enhances local richness [15,16], usually decreases with body mass [17]. That is, large sized taxa are poorly represented in regional pools as compared to small sized ones, and the same species tend to be observed across local communities. Consequently, if the negative density- and regional richness-mass scaling are considered in isolation, α-, β- and γ-diversity of larger sized taxa should be lower than those of smaller sized taxa. In summary, it could be hypothesized the existence of countervailing effects of body size on diversity patterns, which are dependent on the expected influence that the local density scaling, dispersal scaling and regional pool richness scaling have on diversity when they are combined. This framework predicts a negative relationship between body size and β- and γ-diversity due to the reduced number of species that could potentially reach each community from the regional pool, the homogenizing effect of dispersal and the higher local extinction rate of rare species. However, body size could reduce α-diversity because of the higher extinction risk and the lower colonization rate of novel species from the regional pool, but could enhance it because of the higher colonization rates of larger species. Figure 1b shows a visual representation of our hypothesis.

Here we theoretically formalize this hypothesis, exploring the expected interaction between scaling of dispersal, density and regional pool richness as determinants of the diversity–body size relationship. We used a lottery-based metacommunity model that incorporates these three scaling relationships for analysing the expected trends in α-, β- and γ-diversity with taxon body size.

Material and methods

The metacommunity was assembled with a lottery model in two stages (electronic supplementary material, appendix S1 and figure S1). First, communities were filled with coalescent

dynamics starting with the random sampling of one individual from the regional species pool for colonizing each community, and then, filling communities with J individuals each, progressively chosen either from the regional pool, from adjacent communities—neighbouring dispersal—or from the updated community—local recruitment (following [18–20]). After local communities were filled, the lottery dynamics started. At each time step and in each local community, a single individual was randomly removed and replaced with a new one which could also be chosen either from the regional pool, from adjacent communities or from the updated community. Under the lottery dynamics, local extinctions and recolonizations may occur. Dispersal among adjacent (i.e. neighbour) communities was assumed as inversely proportional to the distance between them. This is a spatially explicit model involving neutrality only among species of the same taxon (see [21–24] for similar approximations).

The metacommunity dynamic was simulated for 10 hypothetical taxa representing high-ranking taxonomic groups (e.g. orders), to which a different body size value was assigned. These 10 body size values were uniformly drawn from the interval [1,200]. The model was run considering the potential effect of body size on the parameters representing regional pool richness (S_{pool_i}), local density (J_i) and dispersal ability ($Disp_i$), as

$$S_{pool_i} = aM_i^{b.pool};$$

$$J_i = cM_i^{b.local};$$

$$Disp_{i|p,q} = M_i^{b.disp} * 1/dist_{pq},$$

where a and c are scaling constants, M_i represents the mean body size of the taxon i, $dist_{pq}$ is the geographical distance between communities p and q, and $b.pool$, $b.local$ and $b.disp$ are scaling exponents that relate the richness of the regional pool, local density and dispersal ability of taxon i to its mean body size.

The lottery model was run along gradients of values for $b.pool$, $b.local$ and $b.disp$ that surpassed the range of empirically reported scaling. We run five replicates for each combination of $b.pool$, $b.local$ and $b.disp$. At the beginning of each simulation, a random metacommunity network of 20 local communities was generated. Communities were randomly placed within a landscape in which the geographical distance between each pair of communities could range from 1 to 2000 m. The lottery dynamics were run until both the mean α- and γ-diversity stabilized, eliminating transient dynamics (electronic supplementary material, appendix S1 and figure S2).

For each simulation, we obtained the expected relationship between taxa mean α-, β- and γ-diversity and their body size. It should be noted that γ-diversity refers to the total richness at the metacommunity level, which may differ from the richness in the regional pool. β-diversity was estimated by the difference between the expected value of mean α- and γ-diversity ([25] and electronic supplementary material, appendix S1). We did not include interactions among size–classes in these simulations because our attempt was to visualize the pure effect of the size–scaling on biodiversity. That is, how body size promoted a particular structure of the metacommunity diversity, over which other mechanisms may operate (see [18] for a modelling with size–classes interaction).

We used linear models to evaluate the expected associations between metacommunity α-, β- and γ-diversity and mean body size of taxa. All analyses were performed using R software (v. 4.0.4) [26].
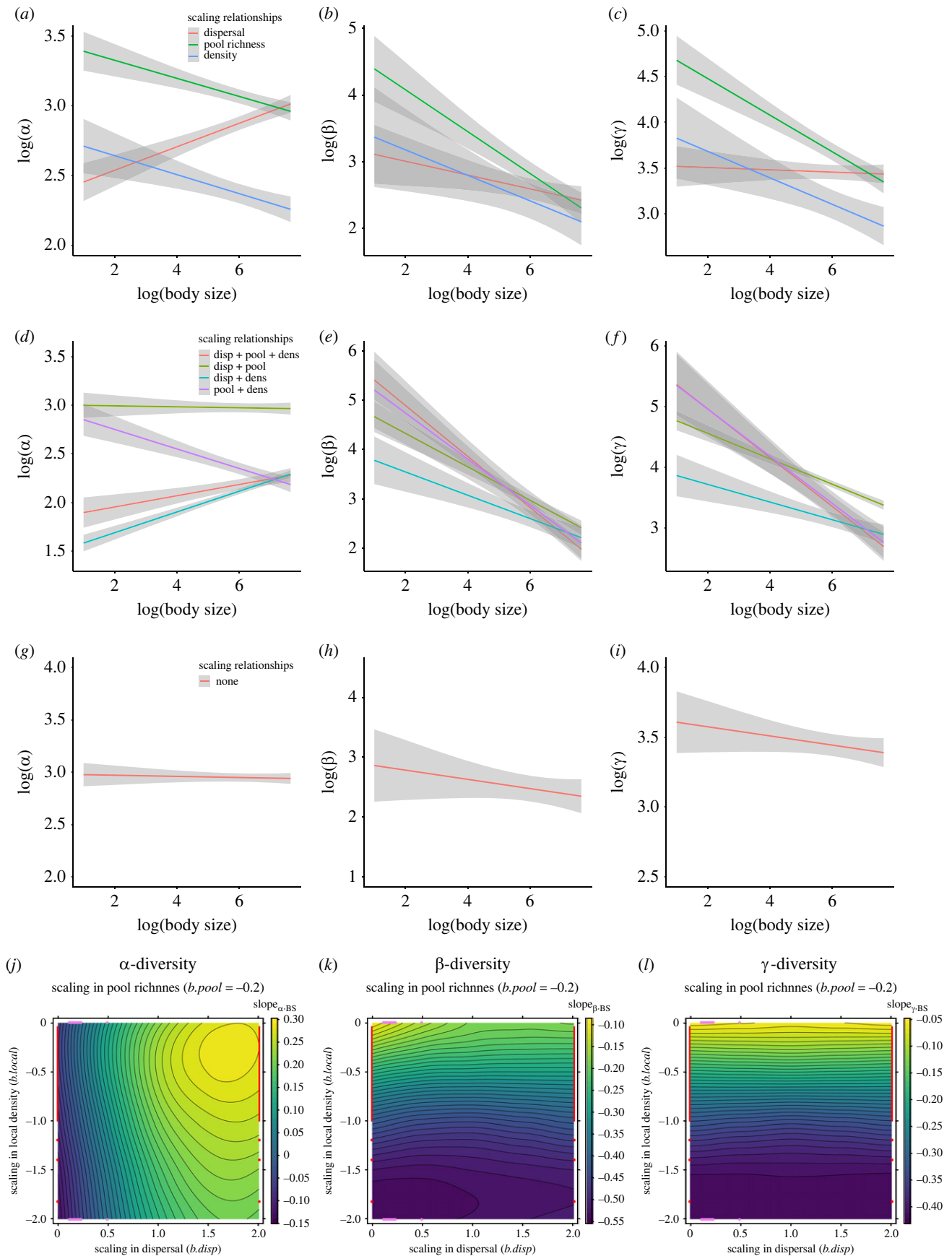
Results

The scaling in dispersal, regional richness and local density with body size affected diversity, both when considered isolated or through their combined effects (figure 2; electronic supplementary material, table S1 and figure S3). When scaling relationships were individually considered, the increase in dispersal with body size enhanced local richness but had negative effects on β- and γ-diversity (figure 2a–c). Conversely, the negative scaling in both local density and regional pool size determined a negative effect of body size on all diversity metrics (figure 2a–c). These results fully matched our expectations (figure 1b). When the scaling relationships were combined, both β- and γ-diversity consistently showed a negative relationship with body mass (figure 2e,f). However, the negative effect of scaling of local density + regional pool richness on local diversity could be reverted when the positive scaling in dispersal ability was considered (figure 2d). Finally, when no scaling relationship was included, body size was not associated with diversity (figure 2f–h). These trends were consistent over a wide range of the parameter space (figure 2j–l; electronic supplementary material, figure S3).

Discussion

In a metacommunity context, the role of body size on shaping diversity has been mainly associated with its effect on taxon-independent dispersal ability [5–7,27]. However, our analyses showed that the interaction among the size-scaling in local density, dispersal ability and regional pool richness may represent a main determinant of the variation in metacommunity diversity among organisms with different body size. That is, our results support that the negative effect of scaling in density and regional pool richness on biodiversity can be counterbalanced by the positive effect of dispersal scaling with body size. While the local richness–body size relationship was qualitatively sensitive to the scaling rule considered, trends in β-, and consequently γ-diversities were not. In agreement with several empirical studies which reported a negative association between dispersal and β-diversity [11], we found a negative effect of the scaling in dispersal on the β-diversity–body size relation. However, a strong effect of the scaling in density and regional richness on the β-diversity–body size association was also captured, a relationship that is poorly considered in the metacommunity literature.

The strength of our modelling approach relies upon its simplicity. Basal neutrality among species of the same taxon, and population dynamics guided by basic ecological processes (i.e. local recruitment, death, dispersal and colonization), allowed us to test our working hypotheses with the minimum of underlying assumptions, which commonly obscure model outcomes. However, some limitations regarding some assumptions of our model should be considered. Simulations were run for hypothetical taxa differing only in body size, although the interaction with other traits could also be important to consider [6,13,28]. A simplified association between dispersal ability and body size was assumed. Nevertheless, variation in dispersal modes suggests that a general scaling may represent a gross approximation to the dispersal ability of each taxon [6]. Additionally, dispersal ability may be nonlinearly related to metacommunity connectivity [29,30] or with changes between life stages [31], determining negative correlations between dispersal distance, frequency and body size. Complex population dynamics and a narrow range of body sizes in local communities may determine weak density–mass scaling at local communities [13,32], but see [33]. The scaling in regional richness with body size may vary among taxa, even presenting unimodal trends [34]. We simulated metacommunity networks with random spatial structures and homogeneous patches. However, more realistic metacommunity configurations can direct dispersal, diminishing the differences in recruitment among taxa [35,36]. Also, local filters could affect the probability of local extinctions [37,38]. These factors may alter the relative effect of each scaling rule in the assembly process. Despite this, the general scaling relationships point to an expected trend in metacommunity diversity with body mass that is congruent with patterns reported elsewhere [39,40]. Our findings suggest that the combination of the three scaling relationships could represent a backbone in metacommunity assembly, upon which the action of idiosyncratic assembly mechanisms and deviations from general scaling rules may operate.

Our focus was on the putative role of sound scaling relationships with body size on metacommunity diversity. In this context, some perspectives deserve attention. First, scaling parameters in ecological rates with body size may differ among systems, explaining differences in diversity among metacommunities, higher taxonomic groups or trophic levels (e.g. [13,41–43]). Second, other biological rates that also scale with mass may be crucial for the regulation of metacommunity diversity [2,44]. Individual turnover rate [45], assimilation efficiency [46], growth rate [47], trophic interactions [48], size and number of dormant structures [49], niche breadth [50] and landscape perception [3,4,29,51] were all related to metacommunity diversity and showed systematic size-dependences. Third, we assumed independence among taxa through our simulations, even though interactions among them could enhance or attenuate expected patterns (see [18]). Fourth, the temperature-dependence of biological rates [52] provides a mechanistic avenue for understanding how climate modulates diversity in a metacommunity framework [2]. Finally, and beyond body size differences, although the model was based on a neutral approach, we also highlight the importance of non-neutral and particularly size-dependent processes in general [4,30]. Consequently, there are several mechanisms by which the integration of metacommunity, niche and metabolic theories may enhance our understanding of biodiversity [22]. Considering biological scaling relationships represents an exceptional opportunity for progress in the mechanistic understanding of the

Figure 2. Theoretical results showing the relationships between diversity and taxon body size. (*a–i*) Expected relationship between α-, β- and γ-diversity with taxon body size for different scaling combinations: (*a–c*) the isolated effects of scaling in dispersal ability, regional pool richness and local density on metacommunity diversity; (*d–f*) combined effects of different scaling relationships; (*g–i*) body size–diversity relation resulting when no scaling relationship was included in the model. Parameter values used in simulations: $a = 100$, $c = 50$, $b.disp = 0.5$, $b.pool = -0.4$, $b.local = -0.75$. (*j–l*) Parameter space for the association between α-, β- and γ-diversity with taxon body size along a gradient in the scaling exponent between local density (*y*-axis) and dispersal ability (*x*-axis) with mass. Pool richness–body size-scaling value (*b.pool*) was set to −0.2. Each point within the parameter space corresponds to the average of the regression slopes between mean α-, β- and γ-diversity obtained from the five replicates run for each parameter combination. Red and purple marginal dots indicate the range of empirical scaling exponents reported in the literature for the relationship between local density and dispersal ability with body mass, respectively (see electronic supplementary material, tables S2 and S3). Patterns are robust to changes in *b.pool* (see electronic supplementary material, figure S3).

interrelationships between body size and diversity in metacommunities, and more generally, for unravelling the mechanisms shaping biodiversity patterns and processes.

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6

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