REVIEWS AND SYNTHESES

Patterns in body mass distributions: sifting among alternative hypotheses

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Abstract

Understanding how animals interact with their environment is critical for evaluating, mitigating and coping with anthropogenic alteration of Earth's biosphere. Researchers have attempted to understand some aspects of these interactions by examining patterns in animal body mass distributions. Energetic, phylogenetic, biogeographical, textural discontinuity and community interaction hypotheses have been advanced to explain observed patterns. Energetic and textural discontinuity hypotheses focus upon the allometry of resource use. The community interaction hypothesis contends that biotic interactions within assemblages of species are of primary importance. Biogeographical and phylogenetic hypotheses focus on the role of constraints on the organization of communities. This paper examines and organizes these various propositions about species body mass distributions and discusses the multiple competing hypotheses, how their predictions vary, and possible methods by which the hypotheses can be distinguished and tested. Each of the hypotheses is partial, and explains some elements of pattern in body mass distributions. The scale of appropriate application, relevance and interpretation varies among the hypotheses, and the mechanisms underlying observed patterns are likely to be multicausal and vary with scale.

INTRODUCTION

Human domination of Earth's ecosystems is transforming the distribution and abundance of the world's biota (Millennium Ecosystem Assessment 2005). This reorganization of the Earth's biodiversity has the potential to affect emergent properties of ecosystems and the provision of ecological services that people depend upon. Thus, understanding how animals interact with their environment is important for recognizing the implications of these changes,

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but acquiring this understanding presents challenges. Numerous processes shape the assembly of animal communities. These processes interact on distinct spatial and temporal scales with emergent features that are difficult to elucidate using reductionist or experimental approaches.

To gain a better appreciation of animal–environment interactions researchers have examined body mass patterns of species from specific communities or systems. Body mass is the most ecologically integrative attribute of a species, and may be a 'taxon-free' attribute (Damuth 1992), thus recognizing patterns in body mass structure can provide clues about the underlying processes affecting community assembly and persistence (Schmidt-Nielsen 1984). Ecophysiologists have demonstrated strong relationships between body mass and a variety of ecological attributes, such as home range and metabolic rates that reveal how body mass relates to the scale at which animals live and use the environment (Peters 1983). Recent work has demonstrated that general fractal structures in the flow of energy and material in plants and animals may underlie some of these allometric relationships (West *et al.* 1997; Brown *et al.* 2004), providing a powerful means for understanding how the ecological relationships between animals and their environment change with scale (Enquist *et al.* 1999).

Examinations of species' body masses in various ecological communities have revealed some consistent patterns (Bokma 2002). Hutchinson & MacArthur (1959) noted that the distribution of body masses among species in assemblages of organisms using similar resources tends towards a log-normal distribution. They suggested that there are more species of small mass because such species can divide habitat into more niches than larger species. May (1978, 1986) gathered data on several different species assemblages and showed that the log-normal pattern is common. More recent examinations have confirmed that many species' distributions are right skewed (Maurer 1999; Gaston & Blackburn 2000; but see Gaston *et al.* 2001). Brown *et al.* (1993) proposed an energetic/evolutionary model of body mass, which predicted a right-skewed distribution that provided a better match to the observed distribution of body masses than did a simple log-normal distribution.

The distribution of animal body masses, and the causes and consequences of patterns therein all focus on particular aspects of the distributions, and are usually contingent on distinct scales of analysis. Many analyses have evaluated overall body mass patterns among organisms, without consideration of species–environment interactions that differ with scale. Many of the features that have the potential to influence body mass distribution change across scales, including vegetation pattern (Krummel *et al.* 1987), evolutionary (Losos & Schluter 2000) and ecological processes (Holling 1992), and the organization of ecological communities (Brown & Nicoletto 1991). These features are not well described by simple allometric relationships, rather they often change abruptly with the scale of analysis (Krummel *et al.* 1987). The ecological and biological literature has been dominated by assumptions that attributes of organisms are distributed continuously, and that such distributions are unimodal. But, although simulated body mass distributions are characterized by even spacing among species, actual body mass distributions exhibit clustering of species (Kelt 1997). This clustering provides some clues regarding the scales on which various competing hypotheses regarding body mass distributions are most appropriately evaluated.

In this paper, we examine and organize multiple competing hypotheses about the distribution of species body mass, and discuss how their predictions vary, and some possible methods by which the hypotheses can be distinguished and tested.

ALTERNATE HYPOTHESES FOR OBSERVED BODY MASS PATTERNS

We have identified five non-mutually exclusive mechanistic hypotheses that describe observed body mass patterns. The hypotheses are: (i) energetic; (ii) phylogenetic; (iii) biogeographical; (iv) textural discontinuity; and (v) community interaction. The energetic and the textural discontinuity hypotheses focus upon the allometry of resource use, while the community interaction hypothesis argues biotic interactions within assemblages of species are of primary importance. The biogeographical and phylogenetic hypotheses focus on the role of geographical and evolutionary constraints on the organization of communities. These alternative hypotheses are discussed in detail below.

Energetic hypothesis

Under this hypothesis, a body mass distribution is taken to reflect the rate at which species can allocate energy to do reproductive work, with modal size species being closer to maximize this rate. This hypothesis predicts one or few modes in body mass distributions at continental scales and is premised on the idea that reproductive ability is limited by the energy acquisition rate from the environment and subsequently by the conversion rate of energy into offspring. A model based on these constraints, allowing unlimited resources and no predation, showed that species body masses would converge on an optimal mass of *c.* 100 g for mammals and 33 g for birds (Brown *et al.* 1993; Maurer 1998b). Competition is suggested as a mechanism that disperses body masses unimodally rather than permitting them to accumulate on the optimum. Since Brown *et al.* (1993) proposed this idea, supporting papers such as Kelt

(1997), Marquet & Taper (1998) and Maurer (1998a,b) have provided additional evidence for the existence of optimal size distributions. Kelt's (1997) model based on fitness constraints yielded an optimal body mass of 100 g when tested with data from mammal communities. Maurer (1998a) tested Brown et al.'s (1993) model for birds and found an optimum body mass of 33 g. If scale-dependent resource variability is introduced into the model, then a single mode can separate into multiple modes (Marquet et al. 1995), indicating an interaction between the distribution of resources in the landscape and body mass aggregations.

Roy et al. (2000) also provide evidence for a unimodal optimum structured by energetics for north-eastern Pacific marine bivalves at the provincial scale, but they did not find evidence that the 'optimum' acts as an evolutionary attractor. Similarly, parasitic nematodes in terrestrial mammals exhibit a log size–frequency distribution that is unimodal and right skewed, reflecting the pattern observed in the mammal hosts of nematodes, and Morand & Poulin (2002) argue that the observed distribution in nematodes is not from phylogenetic effects, but from energetic constraints.

Others have supported the underlying premise of energetic effects on fitness and body mass (Kozlowski 1996), but the assumptions within it have been criticized (Chown & Gaston 1997; Bokma 2001), and some have rejected the model (Perrin 1998; Kozlowski & Gawelczyk 2002). Jones & Purvis (1997) empirically tested the model with bat data and Symonds (1999) tested it with insectivores. Neither study found evidence of an optimal mammal body mass. Evidence of bimodality exists in the fossil record for the last 40 + million years casting doubt on the convergence of all evolutionary lineages upon 100 g (Alroy 1998, 2003). Boback & Guyer (2003) argue that endotherms have a limited capability to become significantly smaller than the optimal size because energetic demands become too unfavourable at smaller sizes. Other empirical tests (Jones & Purvis 1997; Symonds 1999; Meiri et al. 2004) have found no evidence for an optimal body mass.

Kozlowski & Gawelczyk (2002) found that species' body size distributions assume a variety of forms (right skewed, symmetric and left skewed), but right-skewed distributions are most prevalent at large geographical scales (e.g. world, large continent). Body size distributions become more variable at small geographical scales and in narrower systematic groups. They argue that each species has a separate optimum, rather than a taxon-level optimum. In the context of macroevolution, energetics are important, but mortality also plays a fundamental role in shaping body size distributions.

There may be an underlying structure with two or three frequency distributions specific to locomotory modes (plantigrade, digitigrade and unguligrade), with the Afro-tropical assemblages exhibiting trimodal pattern, and the Nearctic assemblage exhibiting unimodality. Lovegrove & Haines (2004) argue that it is unlikely that optimization should produce the same results in different zoogeographical assemblages, because of the tension between mortality and production. Further, they argue that the evolution of diversity in mammal form and function makes a single body size optimum unlikely. Due to the fractal, discontinuous nature of landscapes, the identification of gaps in body size distributions is critical to an energetic definition of fitness, because the gaps reflect specific energetically related body size constraints (Lovegrove & Haines 2004).

The models forwarded by Brown et al. (1993) and Kelt (1997) predict a smooth distribution of body masses, an idea which has been disputed by several authors (Holling 1992; Allen et al. 1999; Havlicek & Carpenter 2001) who describe discontinuous or multimodal distributions of body masses. Holling (1992) and others have shown that the structure of body mass distributions changes with changes in landscape architecture. Bakker & Kelt (2000) reported an additional mode in body mass distributions when comparing North American mammals to South American neotropical mammals, which they attributed to a significant habitat component in the South American neotropics: the rain forest canopy. A body mass distribution manifested as a result of energetic constraints should not change with landscape structure. Energetic constraints are likely to constrain body mass distributions at large spatial and temporal scales, but at smaller and faster scales other mechanisms shape these distributions.

Phylogenetic hypothesis

Several authors have proposed that evolutionary processes constrain the distribution of body mass distributions within taxa and/or that body mass distributions may be composed of faunas with different macro-evolutionary histories, resulting in multiple modes in body mass distributions at continental scales (Gardezi & da Silva 1999; Cassey & Blackburn 2004; Smith et al. 2004). The ancestral forms inhabiting an area limit possibilities for the evolution of their descendants' body masses. For example, comparison of South American mammals deriving from North and South American ancestors reveals that the body mass distribution for South American mammals has three modes. Two of them match modes found in the distribution for North American mammals, and may result from the optimal body mass and the resource limitation hypotheses (Marquet & Cofre 1999). The intermediate mode, however, consists of species that were present in South America before the Great American Biotic Interchange 3–5 million years ago. Although it is currently impossible to know if North American invaders were successful because of the body

mass distribution of South American mammals or if the observed body mass distribution of South American mammals is a consequence of the invasion, it is clear that body mass distributions are made of different faunal stocks with different macro-evolutionary histories.

For fossil North American mammals, the modal body size distribution shifted from low to high size through the Tertiary (Alroy 2000), although the trend reversed towards the end of the Miocene. McShea (1994) has argued that large-scale evolutionary trends in the fossil record are the result of driven or passive forces in bounded spaces. A passive trend is characterized by change that follows the structure (e.g. a boundary constraint) in the established 'state space' (McShea 2000) while a driven trend is one in which the chance of morphological change, speciation and extinction are the same for all lineages throughout the state space. Passive and driven trends are consistent with selection bias and developmental tendencies, and within different contexts (e.g. abrupt or gradual change). If change in body mass distributions is not the result of chance or transient phenomena, then a system is passive, indicating strong ancestral influence upon body mass distributions (McShea 1994). McShea (1994) found evidence for driven mechanisms in horses during the Eocene to the Pleistocene and passive mechanisms in rodents during the Eocene to the Mio-Pliocene. Cumming & Havlicek (2002) used a cellular automaton model to argue that multimodality in body sizes within lineages can arise from the fundamental evolutionary mechanisms of descent and competition.

Phylogenetically independent contrasts reveal that most of the world's mammal species exhibit right skewed body size–frequency distributions (Gardezi & da Silva 1999). At the level of order, right-skewed distributions are found in the smallest size groups. In larger-bodied taxa, right-skewed, left-skewed and symmetric body mass distributions were found in equal proportions. For mammals, the shape of body mass distributions within subclades provides little support for energetic models of body mass distributions (Gardezi & da Silva 1999). North American freshwater fish body size has decreased over time, and the overall body size–frequency distribution is right skewed (Knouft & Page 2003). There are many more small-bodied land bird species on New Zealand, because more ancestral colonizers of New Zealand also were small bodied (Cassey & Blackburn 2004). Those authors conclude that the non-phylogenetic association between small body size and diversity is simply a manifestation of this historical fact. This result is satisfactory for New Zealand, but it does not account for the observation that, on a global scale, most bird species are small bodied, while phylogenetic analyses indicate that the vast majority of ancestral birds are large bodied (Cassey & Blackburn 2004). Size among non-volant terrestrial mammal body masses of congener species over *c.* 18 g exhibited a high degree of heritability across continents and through geological time (Smith *et al.* 2004). This similarity between relatively large mammals is unlikely to have manifested due to the overriding influence of phylogeny. The same relationship was not found for congener species under *c.* 18 g, and Smith *et al.* (2004) argued that life history and ecological parameters are tightly constrained at small sizes, so species can only persist via modifying size. Etienne & Olff (2004) argue that the intermediate modal body size is the result of the trade-off between the allometric scaling law for the number of individuals and the speciation rate decreasing with body size, and the scaling law for active dispersal that increases with body size. However, at the biome scale Sendzimir *et al.* (2003) found no interaction between body mass and taxonomy. At large spatial and temporal scales, phylogeny interacts with energetics to help shape aspects of animal body mass distributions.

Biogeographical hypotheses

These models suggest that multiple modes should be present in body mass distributions at mesoscales because of dispersal (Hubbell 1997), history (Marquet & Cofre 1999) and geography (Hoekstra & Fagan 1998; Silva *et al.* 2001). The limited ability of species to disperse, because of geographical boundaries, may cause a restricted set of species to be present in a given community. Authors have found a positive relationship between geographical range and body mass in many taxonomic groups (Brown & Maurer 1986; Taylor & Gotelli 1994; Gaston & Blackburn 1996; Gutierrez & Menendez 1997; Pyron 1999). These observations suggest that geography and dispersal play as prominent a role in species distribution as the niche-centred theory commonly seen in community assembly analyses (Hubbell 2001). However, others suggest that evolutionary mechanisms and dispersal are the main causes for these observed patterns (Belk & Houston 2002; Knouft 2004). The biogeographical hypothesis is somewhat supported by the fact that different types of species dominate ecosystems that are separated from one another. Marsupials dominate the mammalian fauna of Australia, but are rare in Eurasia. However, the existence of convergent evolution demonstrates that community differences are not solely due to biogeographical separation.

The Core-Taxa hypothesis (Siemann & Brown 1999) suggests that gaps in body mass distributions are due to the differential ability of some species to disperse across biomes. This pattern can be seen across landscapes where there is more turnover in small than in large mammal species (Brown & Maurer 1989; Brown & Nicoletto 1991). Siemann & Brown (1999) described gaps in body mass distributions as biogeographical artifacts. They argued that body masses are a reflection of the distribution of common and

widespread taxa. Siemann & Brown (1999) suggested that body mass distributions at the scale of biomes are influenced by the geographical ranges of species and the history of phylogenetic radiations on a continental scale, and not by biome-specific vegetation and landscape structure, as suggested by Holling (1992). However, the existence of different body mass modes containing different species in adjacent ecoregions that have no obvious boundaries to dispersal (Holling 1992) challenges this idea.

The distribution of body mass on a sub-Antarctic island is bimodal with separate modes for vertebrates and invertebrates (Gaston et al. 2001). In contrast to fractal explanations for species distributions, species richness declined with body size and the scarcity of small species might be a consequence of their large geographical ranges. Rodriguez et al. (2004) assert that the comparison of recent faunas from several continents indicates that body mass patterns of mammals are shaped by biogeographical factors and shifts in body size distributions were not always associated with a shift in habitat structure. They argue that this observation demonstrates that body size is not mainly dependent upon environmental factors.

Phylogenetic effects must be taken into account when investigating patterns in body mass distributions, because turnover is larger for small species than larger ones (Brown & Nicoletto 1991) and studies have demonstrated that geographical range is positively correlated with body mass (Brown & Maurer 1986; Gaston & Blackburn 1996). The range of possible body masses is influenced by evolution. Marquet & Cofre (1999) demonstrated that phylogenetic radiations such as the Great American Biotic Interchange have influenced body masses to some degree in producing unimodal distribution for mammals in North America and a bimodal distribution in South America. Phylogeny affects dispersal as well as energetics, and biogeographical constraints are likely to be manifested selectively among taxa.

Textural discontinuity hypothesis

Holling (1992) proposed that species that function at distinct scales respond differently to the opportunities at these scales, and that the distribution of species' body masses should correspond to the cross-scale distribution of resources within an ecosystem. Holling argued that discontinuities in vegetative pattern and resources should produce a discontinuous distribution of species' body masses, in which body mass aggregations are produced by the availability of resources at different scales. Ritchie & Olff's (1999) observation that, in a fractal environment, species perceive the environment at a scale of resolution which is determined by body size is consistent with Holling's premise. Their spatial models demonstrated that the scaling

of resource use by species of different body size serves as a partial explanation of species diversity across a range of scales. They suggested a relationship between species size and an environment of self-similar habitat, food and other resources.

Numerous analyses of body mass distributions of birds, mammals, herpetofauna, fish and invertebrates have shown a multimodal or discontinuous structure (Restrepo et al. 1997; Allen et al. 1999; Bakker & Kelt 2000; Raffaelli et al. 2000; Havlicek & Carpenter 2001; Kamenir et al. 2004). Research also has revealed that independent attributes of species, including invasiveness, decline, nomadism and migration occur at the edges of these body mass aggregations (Allen et al. 1999; Allen & Saunders 2002).

Many studies have demonstrated that different biomes and landscapes with apparently different ecological structure produce differently patterned body mass distributions (Restrepo et al. 1997; Allen et al. 1999; Havlicek & Carpenter 2001; Allen & Saunders 2002; Sendzimir et al. 2003). Studies by Allen et al. (1999) and Allen & Saunders (2002) have also bolstered empirical evidence by showing that species invading a landscape, species that are declining or extinct, and species that are nomadic tend to be located at the edges of body mass aggregations. However, others have applied different statistical tests to the data presented by Holling (1992) and concluded that the body mass distributions he analysed are characterized by few modes (Manly 1996) or gaps (Siemann & Brown 1999).

Experimentally altering marine sediment assemblages with size-specific perturbations of organic enrichment and predation caused densities and relative abundances of invertebrate taxa to shift, but there was little change in benthic biomass or the abundance size spectrum, maintaining a multimodal distribution of species (Raffaelli et al. 2000). Havlicek & Carpenter (2001) compared body mass distributions in a set of experimental lakes, and reported that despite changes in lake nutrient status and species composition, the multimodal body mass distributions of a wide range of species was conserved.

The three-dimensional structure of habitat provides a strong predictor of the body masses of species dependent upon that habitat (Gutierrez & Iribarne 2004), and others continue to document a relationship between gaps in body size distributions and habitat structure in freshwater fish (Fu et al. 2004), birds (Polo & Carrascal 1999) and nekton (Pittman et al. 2004). Robson et al. (2005) have argued that a re-emphasis of studies on habitat structure and body mass are necessary to refine methodology and synthesize results from pattern seeking and mechanistic research.

Experiments involving manipulated sedimentation in intertidal zones and its effects on body size distributions have produced contrasting results. Schwinghamer (1981) originally suggested that troughs in microfaunal body size

distributions are caused by differences in sediment particle size while Leaper *et al.* (2001) found no evidence for shifts in body size when particle size was manipulated. Raffaelli *et al.* (2000) found that body sizes were conserved when particle size was manipulated suggesting that microfaunal assemblages have well-defined body size distributions shaped by structural features.

Body size distributions are dynamic, and are not characterized by one pattern or category. Stead *et al.* (2005) sampled a range of size fractions of stream benthic metazoans, and documented persistent changes in the number and locations of modes in the distribution, indicating that no single factor determines body size distributions. In particular, they rejected the role of energetics as the sole factor shaping the stream community. In support of the Textural Discontinuity hypothesis, they claim that breaks in body size distributions indicate an abrupt shift in the scale at which species operate in an environment. In contrast to Leaper *et al.* (2001), a pattern of peaks and troughs persisted, regardless of the temporal and spatial variation in the data set (Stead *et al.* 2005). The Textural Discontinuity hypothesis has been identified as a mechanism operating only at mesoscales, and as such operates on species assemblages already shaped by slower and larger processes.

Community interactions hypotheses

Hutchinson (1959) was an early proponent of local community interactions shaping body mass distributions. Interactions involving the defence of resources (Oksanen *et al.* 1979), the exploitation of a common resource (Stubblefield *et al.* 1993) or resource limitation (Nummi *et al.* 2000) influence the distribution of body masses in a community.

Oksanen *et al.* (1979) observed that in species sequences of wading birds from northern Europe the size ratios between the closest species were not constant, leading to the formation of gaps. This observation was in disagreement with the idea that the ratios of body mass should be constant as a result of resource competition, where species have achieved the tightest possible packing on a single niche dimension (Hutchinson 1959; Diamond 1972). To explain their results, Oksanen *et al.* (1979) evaluated three hypotheses, and concluded that gaps were caused by interspecific aggression modulated by habitat structure. Nudds *et al.* (1981) were critical of the study by Oksanen *et al.* (1979), because of the latter's attempt to extrapolate their theory based on European bird assemblages to North American assemblages, and found no gaps in North American dabbling waterfowl or ground-feeding bird arrays based on the classifications in Oksanen *et al.* (1979). Nudds *et al.* (1981) acknowledged that the habitat architecture of North

America and the scale at which these bird species operate does play a large role in shaping body mass distributions.

Predators select prey based, in part, upon size. The selective removal of species within limited size ranges may significantly reduce populations within those ranges, and lead to multimodal distributions in body size (Pennings 1990; Moksnes *et al.* 1998). The resulting body mass patterns for predators and prey should be inverse, with predators creating a 'trophic troph' (Holling 1992). While predation can affect body size distributions and the abundance of species, analysis does not support the existence of trophic trophs (Holling 1992). Stubblefield *et al.* (1993) observed that the size distribution of some prey items of the beewolf (*Philanthus sanbornii*) was multimodal. Among female bees, including both individuals and species, there were three popular sizes separated by two relatively unpopular gaps. The authors concluded that diffuse competition within an assemblage favoured the formation of size guilds (Stubblefield *et al.* 1993) because of the absence of multimodality among prey items that did not feed on pollen. This absence suggested that aspects of pollen foraging produce multimodality.

Resource limitation also may affect body mass distributions. Brown *et al.* (1993) developed a model to explain right-skewed distributions in the body masses of North American mammals. Using a model in which the rate of energy available for reproduction was maximized as a function of body mass, they were able to reproduce the right-skewed distribution in body mass for mammals. This model, however, assumed that resources were not limiting. If resource limitation is included in the model, then the modes shift towards large body masses (P.A. Marquet, unpublished data). This difference can account for the existence of secondary modes that include species with larger body masses. These modes may include species that are resource limited, such as top predators. Alternatively, modes may not be independent from each other. Specifically, modes may represent species belonging to different trophic groups that are linked, such as prey–predator associations (the hitchhiking hypothesis; P.A. Marquet, unpublished data).

Body size distributions for two large assemblages of Costa Rican moths were not right skewed, indicating multiple selective pressures operating on the moths (Agosta & Janzen 2005). There is a correlation between moth body size and the size distributions of moth floral resources, and their results question the search for a single mechanism for the generation of body size distributions. Agosta & Janzen (2005) believe a more realistic view is one in which many dependent mechanisms affect body size distributions at multiple scales (Agosta & Janzen 2005), a conclusion with which we concur. Community interactions may be most important within a context of broader hypotheses, such as

the textural discontinuity or biogeographical. For example, once a species pool or lineage has undergone some level of assembly at broad scales, such as assortment based on the landscape template, community interactions become important and body masses within aggregations follow minimum size ratios (C.R. Allen, unpublished data). Thus, within a community, the distribution of differently sized species can be shaped by interspecific interactions, resulting in non-random distributions of varying form at local scales.

SIFTING AMONG THE ALTERNATIVE HYPOTHESES

All of the hypotheses discussed predict modality or discontinuity in body mass distributions. The phylogenetic and biogeographical hypotheses emphasize the role of limits, those of evolutionary constraints upon body forms or constraints upon dispersal and species mixing. Thus, those two hypotheses focus upon the role of historical contingency. The energetic and textural discontinuity hypotheses emphasize interactions with resource availability and distribution. The energetic hypothesis focuses upon limits of available resources and the optimal body mass for resource utilization, and the textural discontinuity focuses upon how the distribution of resources differs at different temporal and spatial scales. The community interaction hypothesis is distinct from the other four hypotheses in focusing upon interspecific interactions.

These competing hypotheses differ in the spatial and temporal scales at which they can make useful predictions (Fig. 1). The energetic and phylogenetic hypotheses are best applied at broad scales, the biogeographical and textural discontinuity hypotheses at intermediate scales and the community interaction hypothesis at the local scale. The body mass of a species, and the distribution of body masses

in a system, reflects multiple processes operating at many different scales, which may explain much of the controversy over the best theory to explain patterns in body mass distributions. Comparisons of body mass patterns at different spatial scales should reflect processes at distinct scales if we are to differentiate among alternative hypotheses. However, we note that while spatial and temporal scales are often disconnected in the literature, for the purposes of understanding body mass distributions it is best to consider them in concert. Our ability to simultaneously test these hypotheses is generally constrained to analyses of observational data, but limited experimentation is possible in some cases. However, because of the practical limits to replicated manipulation, and likely multicausal drivers of pattern, our approach is not to ask which of these hypotheses are true, as they are all true in a trivial sense. Rather we ask which hypothesis or combination of hypotheses best explains the patterns observed in biological communities.

A critical issue to be resolved before confronting alternate hypotheses with data is determining how to rigorously quantify patterns in body mass distributions, and compare different distributions. Few rigorous methods exist for the detection of such pattern (Allen & Holling 2001). For example, how much of a shift is necessary to say a mode or gap in a distribution is in a new location when comparing body mass distributions? The methodological choice should depend on the inherent variation in body mass of the group being compared, and should focus on reducing Type II rather than Type I error (Holling & Allen 2002). Despite suggesting substantially different causative mechanisms, all hypotheses accept the presence of pattern in body mass distributions. Thus, one should use methods sensitive to the detection of that pattern. Ideally it is best to use multiple methods and search for convergence on the most likely interpretation of pattern (Fig. 2). Additionally, different
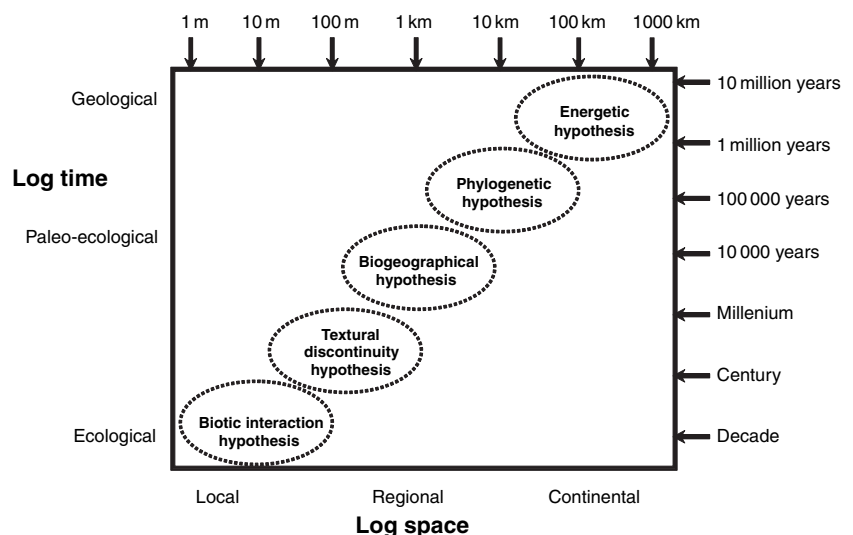

Figure 1 The scales at which the mechanistic hypotheses explaining animal body mass patterns are likely to predict the pattern of body mass distributions. This figure shows no overlap among hypotheses, but we perceive both the spatial and temporal dimensions of adjacent domains as interacting. We also believe that mechanisms acting at larger and slower scales provide non-random species pools upon which faster and smaller mechanisms work.
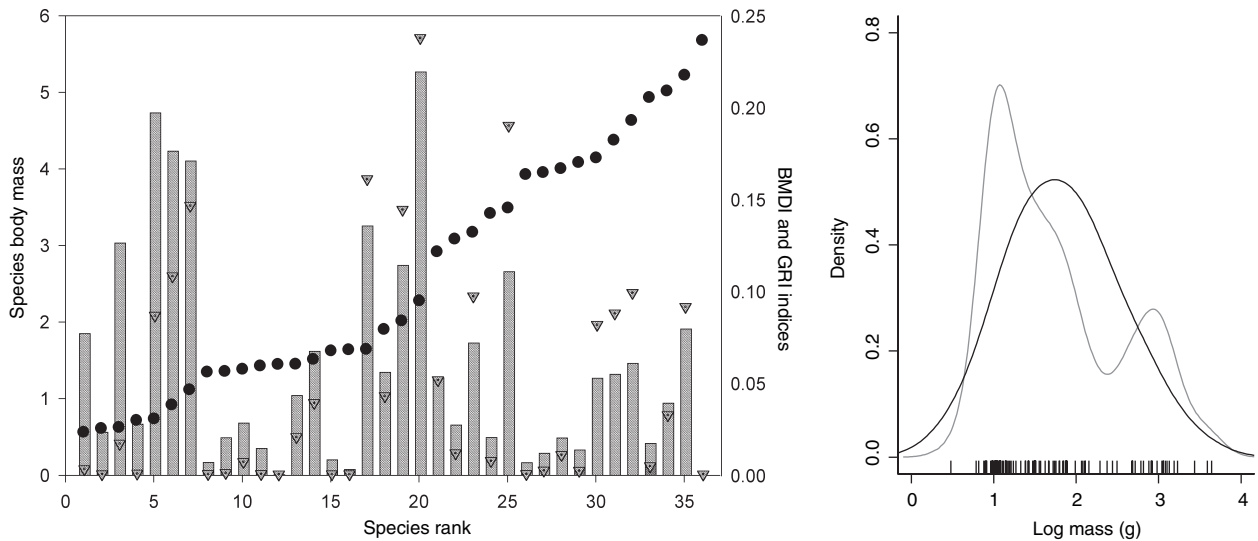
Figure 2 Some of the patterns possible in body mass distributions, illustrated with a well-known example (Holling 1992; graphic modified from Holling & Allen 2002). The left graphic shows species rank vs. body mass (left *y*-axis, circles) and split moving window (Mn/Mn + 1; vertical bars, right *y*-axis) and gap rarity indices (triangles, range 0–1, axis not shown). Where body masses of adjacent animals are very similar, the line represented by the circles is nearly flat. Large differences in body masses are recognized by jumps. Similarly, high values for both indices indicate 'gaps', unusually large size differences between adjacent species. More familiar statistical procedures, cluster analysis and classification and regression trees provide qualitatively the same results. The right panel shows the density curve for Holling's boreal bird data (the curve with the high peak). Also shown is the unimodal density curve for a sample of the same size drawn from a lognormal distribution with mean and SD similar to Holling's data. The black lines on the *x*-axis represent each observation.

underlying hypotheses suggest different approaches. Hypotheses that predict underlying zones of attraction suggest the use of tests for multimodality, whereas hypotheses that suggest that there are 'forbidden zones' (gaps) invite tests for discontinuities.

PREDICTIONS FROM ALTERNATIVE HYPOTHESES

There are contrasts that may distinguish among the different predictions that follow from the hypotheses presented and the dominant mechanisms suggested by each of the five hypotheses (Table 1). In comparisons, one variable should be changed while others are held constant. In doing so, one may determine which factor is the greatest driver of the observed pattern in body mass distributions. It may not be possible to obtain data sets to construct all such comparisons, but this approach is a useful framework to examine the relative veracity of each of the five hypotheses. We discuss these contrasts below.

Response to change in species or change in ecological structure

There are at least two ecosystem comparisons that can distinguish among the hypotheses. The first is to compare body mass patterns among systems with similar ecological structure, but with faunas that have been evolutionarily isolated. Mediterranean climate ecosystems best approach this condition. In such comparisons, both the energetic and the textural discontinuity hypotheses predict that the body mass distributions in the ecosystems will be similar. In contrast, the community interaction, biogeographical and phylogenetic hypotheses predict that because of different community composition or geographical and evolutionary barriers to dispersal, the body mass patterns between the systems being compared will be different.

The second comparison that may help distinguish between competing hypotheses is a comparison of adjacent ecosystems with different structure. In such a comparison the landscape structure will be different, but the taxonomic identities of species and their evolutionary histories will be similar, even if there are differences at the species level. In this comparison phylogenetics are held constant and pairs of ecosystems are compared that are spatially connected to allow dispersal, but they have different habitat architecture (e.g. deciduous forest and grassland). Here, the community interaction and textural discontinuity hypotheses predict differences in body mass patterns. The community interaction hypothesis predicts that differences in the taxa present will lead to different patterns, but because taxonomic differences are expected to be restricted to the species level, differences in body mass patterns are expected to be slight.

Table 1 Change in body mass distributions following changes in taxa, location or landscape structure

| Hypothesis | Stasis | Change in species or structure | | Response to perturbations | |
		Change in species across systems with similar structure	Change in structure across systems with similar species	Biological invasions	Change in landscape structure
Energetic	Unimodal	No change	Minor change	No change	No change
Community interaction	Multimodal	Idiosyncratic change	Idiosyncratic	Idiosyncratic	No change
Biogeographical	From few to unimodal	Idiosyncratic	Minor change	No change	No change or fill gaps
Phylogenetic	Few modes	Idiosyncratic change	Minor change	No change	No change
Textural discontinuity	Multimodal	No change	Change in aggregation number and location	No change	Change in aggregation number and location

Stasis refers to the expected state of a body mass distribution in the absence of perturbation. Change in species across systems with similar structure occurs, for example, when we compare Mediterranean climate ecosystems from different areas of the world. Change in structure across systems with similar species occurs when comparing different adjacent ecosystems.

The textural discontinuity hypothesis, however, predicts substantial differences in body mass patterns in this comparison because the structure available to animals differs. The energetic, biogeographical and phylogenetic hypotheses all predict no, or very small, differences in pattern between the two systems because there are no geographical or phylogenetic barriers that would limit certain body masses.

Responses to perturbations

Two fundamentally different (but often non-exclusive) perturbations can affect an ecosystem: those that directly affect ecosystem processes, and those that directly affect species composition. Although a change in one component of an ecosystem may cause changes in the others, it is useful to find examples that directly change only one component at a time. The alternate hypotheses propose different degrees of resistance to different perturbations (Table 1), and these different perturbations have different implications within the context of each hypothesis.

First, consider a change in an ecosystem process that does not directly change habitat architecture, for example, an increase in nutrient availability to an ecosystem such as a deciduous forest. The textural discontinuity hypothesis predicts that although the abundance and identities of species will likely shift, the overall body mass pattern will be conserved. The community interaction hypothesis predicts that there will be differential responses by different members of the community as competition for some resources is alleviated while other resources become limiting. There will be an overall shift in the community dynamics and thus a change in the body mass pattern. The biogeographical, energetic and phylogenetic hypotheses predict that there will not be an effect on body mass patterns at shorter time scales unless there is considerable change in the phylogenetic background of the community through immigration, emigration or extinction.

Another useful comparison considers a change in physical structure that does not change processes. For example, the removal of midsize patches in an otherwise continuous forest network. The textural discontinuity hypothesis posits that species masses are linked to habitat architecture at discrete scales, so it predicts that a body mass aggregation that is scaled to midsize structure should disappear. The community interaction hypothesis predicts that there will be no change in body mass distribution, as species composition is unlikely to change. The same is true for the energetic, biogeographical and phylogenetic hypotheses, because such a change in structure will not change phylogeny of the species present or the connectivity of the system.

Systems may be perturbed by the introduction of non-indigenous species. The textural discontinuity hypothesis suggests that body mass patterns do not depend on the identities of species present. So, although the abundance and composition of species may change following species turnover (i.e. invasions and extinctions), the overall pattern will be conserved. Thus, the textural discontinuity hypothesis predicts little or no change in body mass patterns with invasions. Likewise, the energetic and phylogenetic hypotheses predict minimal change with invasions, because differences in species composition are irrelevant to the underlying constraints of phylogeny or energetics. The biogeographical hypothesis predicts little change with few invasions, to a filling in of gaps in body mass distributions with a large number of invasions. The community interaction hypothesis predicts that body mass patterns will change because species interactions will change.

Response of different taxa and trophic groups on the same landscape

Comparing different taxonomic groups (e.g. birds, mammals and reptiles) that live in the same ecosystem will lead to different predictions under the various hypotheses. This comparison holds habitat architecture and geographical contiguity constant while varying phylogenetics. The biogeographical hypothesis predicts the body mass patterns among groups will be different because they are phylogenetically unrelated. However, geographical legacy cannot be separated because all groups are in the same habitat. The phylogenetic hypothesis also predicts different patterns in different taxonomic groups because its parameters are phylogenetically determined. The textural discontinuity hypothesis predicts that different taxonomic groups will have a similar discontinuous pattern. If body mass pattern is controlled by landscape architecture, changing phylogenetics will not significantly change the pattern because all animals must exploit the same resource matrix. The community interaction hypothesis predicts that evaluation of different taxonomic groups or even guilds, within the same system will yield different patterns because different sets of species will interact differently.

Alternatively, a comparison of closely related taxonomic groups living in different landscape types holds phylogenetics constant while changing habitat architecture. The choice of habitats will determine the control over geographical contiguity effects on dispersal (immigration and emigration). The best comparisons would result from comparing regions with similar dispersal opportunities, and especially regions that are currently geographically contiguous. However, clearly if there is phylogenetic overlap, the habitats were physically or functionally connected for at least some period of time. In this case the biogeographical and phylogenetic hypotheses predict that there will be conservation of pattern because phylogenetics are held constant, while the textural discontinuity and community interaction hypotheses predict changes resulting from different habitat architecture. Although the species identities may be close phylogenetically, they are competing for different resources so their interactions should be different.

Response to differing scale

The most useful method to change spatial scale will be to continuously aggregate species from regions that are geographically contiguous. There are then two different methods of aggregation, which may lead to different results that can distinguish among the competing hypotheses. First, one could aggregate animals from a single ecosystem type before adding species from a different type of ecosystem. For example, aggregate all open woodland systems before adding tropical swamp or prairie grassland species. Second, one could aggregate along habitat gradients, where species in geographically contiguous regions are combined while crossing ecosystem boundaries. If body mass patterns are determined by species identities interacting for resources more so than the habitat architecture of the resources, we expect less change as we cross a landscape boundary with phylogenetically similar species than when staying within the same system.

The textural discontinuity hypothesis predicts that the discontinuous pattern will be conserved when aggregating discrete units of a single ecosystem type until the addition of different ecosystem types blurs discontinuities. The biogeographical hypothesis predicts the discontinuous pattern will be conserved until a phylogentic and/or dispersal boundary is crossed. The community interaction hypothesis predicts the discontinuous pattern will change with species identities and habitat types, so the pattern should change at a smaller scale of aggregation than either the textural discontinuity or biogeographical hypotheses. The phylogenetic hypothesis predicts a unimodal distribution based on phylogenetic optimization. However, different phylogenetic lineages may mix, leading to the shifting of modes or multimodality.

Response to temporal change

Temporal change is systematic change over time, such as climate warming/cooling, precipitation trends, increases or decreases in nutrient loading, and population numbers increasing or decreasing. These are (often) gradual shifts in system variables or parameters. The response of the ecosystem to these changes may depend on the sensitivity of a critical threshold.

The textural discontinuity hypothesis predicts that if gradual temporal change does not reach a threshold, the pattern in body mass distributions will be resistant to change. Once a threshold (i.e. system resilience) has been exceeded, the whole system should reorganize to a new system state. The community interaction hypothesis predicts that we should see a more continuous change in the pattern of aggregations and discontinuities. In contrast, the phylogenetic and the biogeographical hypotheses predict no change in body mass distributions because evolution does not work fast enough to produce change unless some threshold has been exceeded resulting in mass extinction, such as occurred during the Pleistocene (Lambert & Holling 1998).

WEIGHT OF THE EVIDENCE

Interpretation of patterns in body mass distributions, as well as methodological approaches, differs based on whether there is multimodality in the distributions or discontinuity.

The existence of multiple modes suggests multiple attractors whereas discontinuities suggest areas of repulsion. It is reasonable to believe that the processes leading to pattern vary with scale, and that at some scales repulsive processes are responsible and at other scales attractive processes are responsible. Regardless, analyses of body mass distributions have discovered pattern using both tests of multimodality (Havlicek & Carpenter 2001) and discontinuity (Allen *et al.* 1999). There is now good evidence for the existence of multimodality or discontinuity in body mass distributions, and the focus is now upon mechanistic explanations for observed patterns.

Roy *et al.* (2001), reporting from the fossil record, found that marine bivalves shifted their geographical ranges in response to climate change. The species that made these moves were larger species in the regional body size–frequency distributions. Importantly, these shifts were not attributable to phylogenetic effects, ecological categories or types of reproduction and larval development (Roy *et al.* 2001). Size-based macro-evolutionary processes and the fractal or discontinuous nature of the environment can be complementary and help to explain body mass patterns in consort (Kozlowski & Gawelczyk 2002).

In this paper, we have characterized the dominant competing mechanistic hypotheses explaining pattern in body mass distributions. Each of the hypotheses explains elements of pattern in body mass distributions. Their relevance, however, varies with the scale at which the hypothesis is applied, as there is no evidence that one scale is superior to an alternate scale of analysis (Vermaat *et al.* 2005). The community interaction hypothesis explains proximate interactions among species at the spatial extent of local landscapes. The textural discontinuity and biogeographical hypotheses operate on similar temporal (paleo-ecological) and landscape (regional) scales, yet imply different mechanisms for the manifestation of body mass distributions. The phylogenetic and energetic hypotheses explain temporally slow and spatially broad patterns best, such as the patterns in body mass distributions observed at continental scales.

Thus, it appears that each of these hypotheses explains part of the puzzle. Only by utilizing a multiscale framework can we hope to unravel the relationship between body size distributions and the cross-scale processes affecting those patterns (Krawchuk & Taylor 2003). To link processes to body mass patterns, the scale of the analysis is the critical variable (Shen *et al.* 2004). It is likely that different processes are important at different scales, and no single theory is likely to account for patterns at different scales (Holling 1992; Gaston *et al.* 2001). The scale of appropriate application, relevance and interpretation varies among the hypotheses, and the mechanisms underlying observed patterns are likely to be multicausal and vary with scale.

The mechanisms identified by each of the five hypotheses have support, and understanding the scale domains of each, and how they interact across scales, will help ecology provide an understanding of the distribution of biological diversity in space and time.

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