III.16

Macroecological Perspectives on Communities and Ecosystems

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Macroecology is an emergent research program in ecology that examines patterns and processes in ecological systems at large spatial and temporal scales. It acknowledges the complexity of ecological systems and the limitation of reductionistic approaches, emphasizing a statistical description of patterns in ensembles of multiple species. One of its goals is the identification of regularities that might eventually unveil the general principles underlying the structure and functioning of communities and ecosystems.

GLOSSARY

energetic equivalence. Concept that denotes the equivalence of species in terms of the amount of energy that their populations use within natural communities

metabolism. Network of chemical reactions that take place in living entities and by which energy and materials are taken up from the environment, transformed into the component of the network that sustains it, and allocated to perform specific functions

metacommunity. Set of local communities that are linked by the dispersal of their components and potentially interacting species

metapopulation. Set of local populations of one species linked through dispersal

reductionism. Scientific approach by which understanding of complex systems can be obtained by reducing them to the interactions among their constituent parts

scaling. Name given to the existence of a power–law relationship between two variables of the form $y=ax^{\theta}$, where θ is the scaling exponent and is normalization constant

species–area relationship. Relationship that describes how the number of species increases with the area sampled or with the size of the system under analysis (e.g., lake, habitat fragment, or island)

Theory of Insular Biogeography. Equilibrium theory proposed by MacArthur and Wilson in 1963 that proposes that the number of species in a given island results from the dynamic equilibrium of the opposite processes of immigration from a source and local extinctions

1. THE ROAD TO MACROECOLOGY

As do most research programs in science, macroecology represents the crystallization of a line of inquiry that started two centuries ago with the discoveries of the German naturalist Alexander von Humboldt, published in 1807, and his remarks on the latitudinal distribution of biodiversity (the pole-to-tropic gradient) and continued, with different intensity, in the works of Olof Arrhenius, Carrington Bonsor Williams, John Christopher Willis, Frank Preston, Leigh Van Valen, George Evelyn Hutchinson, Robert MacArthur, Eduardo Rapoport, and several others. One can ask in retrospective, What makes the work of these authors macreocological? The common theme in all of them was the usually large spatial extent (i.e., regional to continental) of the patterns they reported and the use of statistical descriptions of species ensembles with regard to attributes such as abundance, richness, geographic distribution, or body mass, with an emphasis on the emerging patterns rather than on the component

species. Before macroecology, these patterns were studied in isolation and interpreted as resulting from evolutionary processes and/or ecological or biogeographic dynamics. Macroecology provided a synthetic and common framework for all of them by explicitly recognizing the importance of, and the links among, ecological, evolutionary, and biogeographical processes and scales in the understanding of ecological phenomena.

Three major events contributed to the consolidation of macroecology as a research program in ecology

1. First is the recognition of the role played by regional factors in affecting the local dynamics of populations and communities. The importance of regional effects became recognized thanks to the analysis of the degree of coupling between local and regional diversity championed by Robert Ricklefs and the development of metapopulation theory, which, although formally introduced in 1969 by Richard Levins, started to flourish in the 1980s, most notably through the work of Ilkka Hanski.
2. As we elaborate in greater detail below, macroecological work is usually concerned with patterns occurring at regional to global scales where experiments are not feasible and data are difficult to obtain. However, this changed during the last two decades with the explosive development and/or availability of data such as atlases on the distribution and abundance of different taxa (e.g., Breeding Bird Survey, Gentry Plots) and the development of new technological tools to deal with and to generate data on environmental variables at large spatial scales (e.g., satellite imagery, remote sensing, and geographic information systems).
3. Finally, one the main drivers of the macroecological approach was the growing recognition of the limitation inherent to the reductionistic, microscopic approaches that became dominant in ecology since the 1970s, which try to understand ecological communities from detailed knowledge on between-species interactions through manipulative experiments of short duration and limited spatial extent.

Reductionistic approaches, although powerful in characterizing the outcome of pairwise species interactions at a given locale, cannot deal appropriately with the vexing complexity of ecological systems composed of networks of many species, linked through direct and indirect paths of different strengths and degrees of nonlinearity, and subjected to processes acting at different temporal and spatial scales (e.g., species extinction and speciation and individual birth, death, and dispersal). In this context, it comes as no surprise that communities, under the microscopic paradigm, were considered as highly variable and idiosyncratic with regard to the relative importance of specific biotic interactions (e.g., competition, predation, mutualism) and their effect on local coexisting populations. Two representative quotations from major figures in the field of ecology can help us to clarify this point. Lord Robert May, in his MacArthur Award address published in the journal *Ecology* in 1986, wrote: "Ecology is a science of contingent generalizations, where future trends depend (much more than in the physical sciences) on past history and on the environmental and biological setting." This view was also sponsored by two prominent community ecologists, Jared Diamond and Ted Case, who in the introduction to the edited volume *Community Ecology,* wrote:

> The answers to general ecological questions are rarely universal laws, like those of physics. Instead, the answers are conditional statements such as: for a community of species with properties A_1 and A_2 in habitat B and latitude C, limiting factors X_2 and X_5 are likely to predominate.

2. MACROECOLOGY: TOWARD A DEFINITION

Most people are unaware that the first use of the word *macroecology,* curiously, appeared in a small monograph published in Spanish in 1971 by Guillermo Sarmiento and Maximina Monasterio, two Venezuelan researchers working in tropical savanna ecosystems. They used the word macroecology to mean the analysis of broad patterns in vegetation that resulted from the interaction between geomorphology and soil properties at large spatial scales (between regional and landscape scales). They compared this approach with what they called microecology (by analogy with the distinctions made in economics between macro- and microeconomics), which they characterized as a detailed inventory of species abundance and composition at small (plot) scales. The research program we usually call macroecology, however, was formally introduced in 1989 in a seminal paper by James H. Brown and Brian A. Maurer. They defined macroecology as the study of how species divide resources (energy) and space at large spatial scales, with its goal the study of the assembly of continental biotas. By undertaking analyses at this large spatial scale, they expected that local idiosyncratic noise would tend to cancel out so they would be able to pick up the fingerprint of general

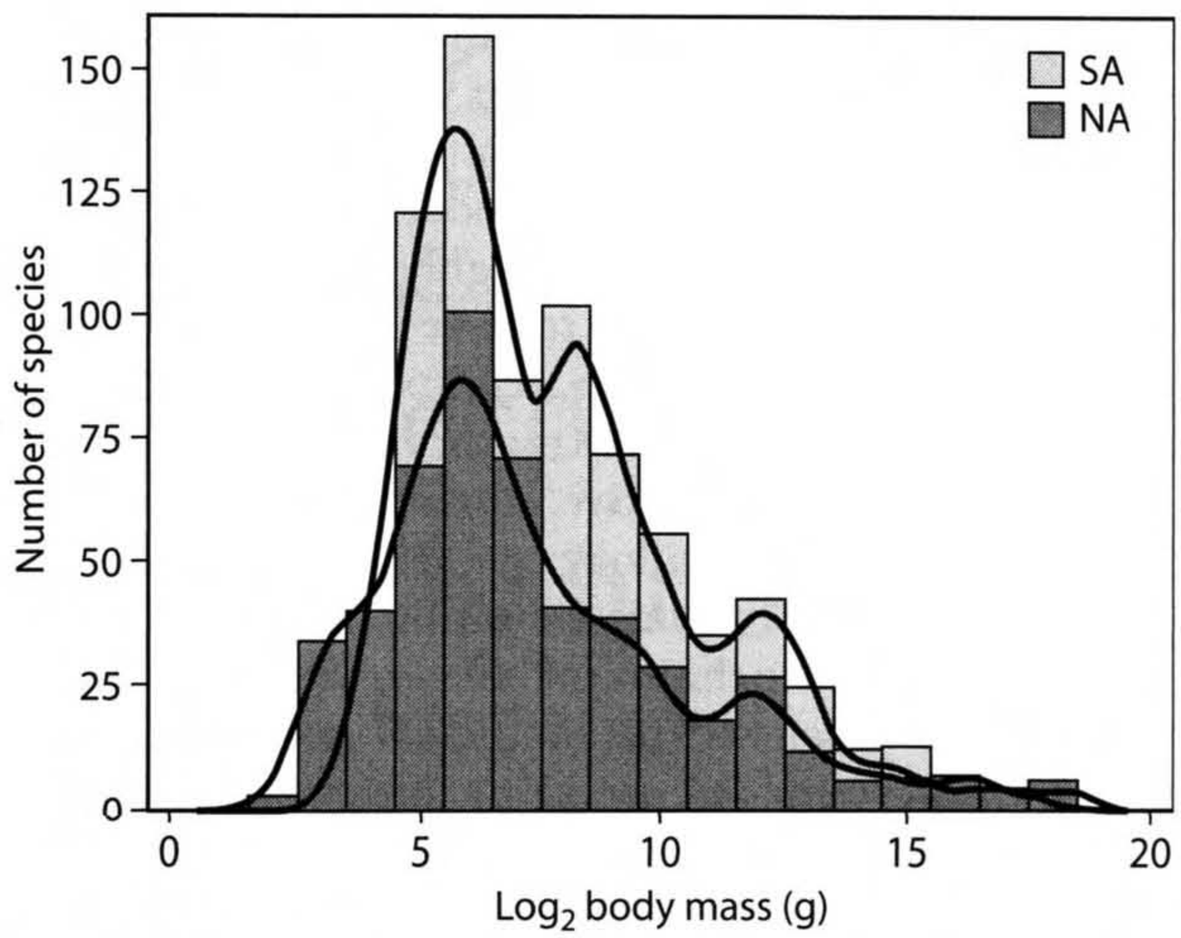

Figure 1. Body size distribution for North American (NA) and South American (SA) terrestrial mammals. The continuous lines represent the result of applying a kernel smoothing to reveal the complex structure of these distributions with lumps and gaps in body size. (After Marquet, Pablo A., and Hernán Cofré. 1999. Large temporal and spatial scales in the structure of mammalian assemblages in South America: A macroecological approach. Oikos 85: 299–309)

patterns and principles affecting ecological systems (figure 1).

After its original definition, the term *macroecology* has taken different meanings. The two most commonly in use are (1 macroecology as the study of biodiversity patterns and processes at large spatial and long temporal scales, a sort of large-scale community ecology, and (2) macroecology as a sort of statistical mechanics, where the emphasis is on the statistical regularities that emerge from the study of ensembles or large collections of species, about which it tries to make the fewest possible assumptions, the same as with particles in statistical mechanics. Under this definition, macroecology is concerned with the existence of statistical patterns in the structure of communities that seemingly reflect, or might provide some clues on, the operation of general principles or natural laws. This makes of macroecology, to some extent, a radical (from the Latin radix = root) attempt aimed at understanding ecological systems from first principles.

3. MACROECOLOGICAL PATTERNS

Macroecologists have analyzed a myriad of patterns in biodiversity As would be expected in any research program at its early stages, large efforts have been placed in the documentations of patterns, which serve as the empirical foundations on which deductive and prediction-rich theories rest. It is beyond our scope here, however, to describe and provide an in-depth discussion of each of the patterns that macroecologists most commonly work with, but for the sake of simplicity, those patterns can be separated into three categories.

Patterns in the Frequency Distribution of Ecological Attributes

As is usually emphasized in descriptive statistics, knowledge of the shape of the frequency distribution of the variables under study is of paramount importance, as it not only informs us if the data fit the assumptions required by statistical tests but may also shed light on the type of processes that underlie its emergence. Macroecologists have been deeply concerned with the shape of frequency distributions of traits such as body size, abundance, and distribution and how these change across time and space (figure 1). Important questions that macroecologists have tried to answer are related to, for example: What determines the size of the largest- and the smallest-sized species found in a given biota? Are there gaps in body size distributions? Why are most species of small to medium size? How much does this distribution vary across time and/or from local to global scales? And do other taxa, such as trees, bacteria, or birds show similar distributions? So far, very few of these questions have a definitive answer. We know, for example, that the area of a landmass determines the size of the largest species that can potentially evolve there and that the shape of the body size distribution is highly variable across space and taxonomic groups. Just as with other macroecological patterns, body size distributions are affected by how speciation and extinction rates vary with body size and by how the strength and direction of these relationships are affected by environmental factors such as temperature and area. However, as of yet, macroecologists are far from achieving a general explanation for body size patterns, one that is not only able to explain the patterns we already know but can at the same time predict new patterns in size distributions across time, space, and taxa.

Patterns in the Covariation of Attributes

Patterns in covariation have been widely analyzed by macroecologists. Among them are the famous relationship between local and regional species richness and that between density and body mass (figure 2), among many other ecological and life history traits that covary with individual size, such as geographic range, home range area, population variability, and lifespan,

which have been thoroughly documented in several books such as Robert Henry Peters (*The Ecological Implications of Body Size*) and William Alexander Calder III (*Size, Function and Life History*), both published in 1983, and more recently, in 1994, Karl Joseph Niklas (*Plant Allometry*).

The relationship between population density and body size has a long history in ecology Carl O. Mohr originally proposed it in 1940, in the context of analyzing wildlife census techniques. He reasoned that a plot in which different estimates of density are plotted for each species would allow one to assess what he called economic densities (i.e., the number of individuals per unit of habitat actually used by the species) and thus compare the estimates of alternative census techniques. Mohr, however, did not pay too much attention to the biology in this relationship. It was not until 1981 that John Damuth revisited it and showed that population density of herbivore mammals decreased with body size and that density was related reciprocally to individual metabolic requirements, implying that different species, regardless of their size, tend to use similar amounts of energy within communities. We revisit and expand on this relationship in a later section.

Patterns of Change in Attributes along Time or Space

Probably the best-known macroecological patterns in time and space are those between species richness and latitude and the well-known relationship between species richness and area. These patterns, although well documented for a variety of taxa, still remain an active area of inquiry. For example, the latitudinal pattern in species richness (figure 3) has been reported in a great diversity of organisms, from microbes to trees and vertebrates, and it is known to occur in terrestrial, marine, and freshwater environments. Ultimately, the gradient should reflect latitudinal variations in rates of speciation and extinction. The prevailing view is that most species originated in tropical areas, which served as the "cradle of diversity," and that a large fraction of them have remained there, meaning that it has also served as a "museum of diversity " The reasons why speciation is high and extinction low in the tropics, however, are still much debated, as many biotic and abiotic factors, such as temperature, productivity, and area, can affect these rates.

Macroecologists have also focused on some of the so-called ecogeographic rules such as Bergmann's rule, which refers to the tendency for individuals of a given species to increase in size toward the cooler areas of its geographic range. Other well-studied patterns are the tendency for lineages to increase their size over geological time (i.e., Cope's rule) and the tendency for small species to evolve toward larger size (gigantism) and large species to evolve toward smaller size (dwarfism) in islands (the island rule). But not only patterns in the temporal and spatial variation of morphological traits are within the domain of macroecology; the way population density changes across the geographic range of a species has also been the focus of much research, as has the temporal dynamics of ranges themselves (i.e., their expansion and collapse) as well as geographic patterns in the size and shape of geographic ranges.

There is no doubt that macroecology is rich in patterns. The discovery of patterns and their statistical description, however, are the beginning of a process whose end is the proposition of a hypothesis about mechanisms that could potentially give rise to the observed phenomenon. The history of ecology tells us that the time it takes to traverse this path, from the identification of a general pattern to the proposition of generative mechanisms, is usually long and is marked by bursts of activity reflected in the generation and coexistence of several alternative models and hypotheses that can explain the same phenomenon. And this is true for most macroecological patterns. Two recent theoretical developments [the Metabolic Theory of Ecology (MTE) and the Neutral Unified Theory of Biodiversity (NUTB)], however, have shown that several macroecological patterns are interconnected and can, as a first approximation, be understood as resulting from the action of simple and general principles. As we will see in the next section, these theories have revolutionized the field, highlighting the simplicity underlying complex ecological systems.

4. NEUTRAL MACROECOLOGY

Neutral theories have a long history in biology Motoo Kimura introduced the first neutral model within biology in the 1960s. This neutral model was intended as a vehicle for understanding the forces affecting allelic variation in the context of population genetics. The neutral theory of population genetics asserts that most allelic changes in a population are selectively neutral, or nearly so, and driven by mutation, migration, and genetic drift. Although originally viewed as an anti-selectionist theory, it is now appreciated as an important complement to our understanding of the factors driving adaptive evolution. The application of these ideas to understand patterns in ecological systems dates back mainly to the work of Hal Caswell, who, in 1976, developed a neutral theory in the context of community ecology with the goal of understanding the role of

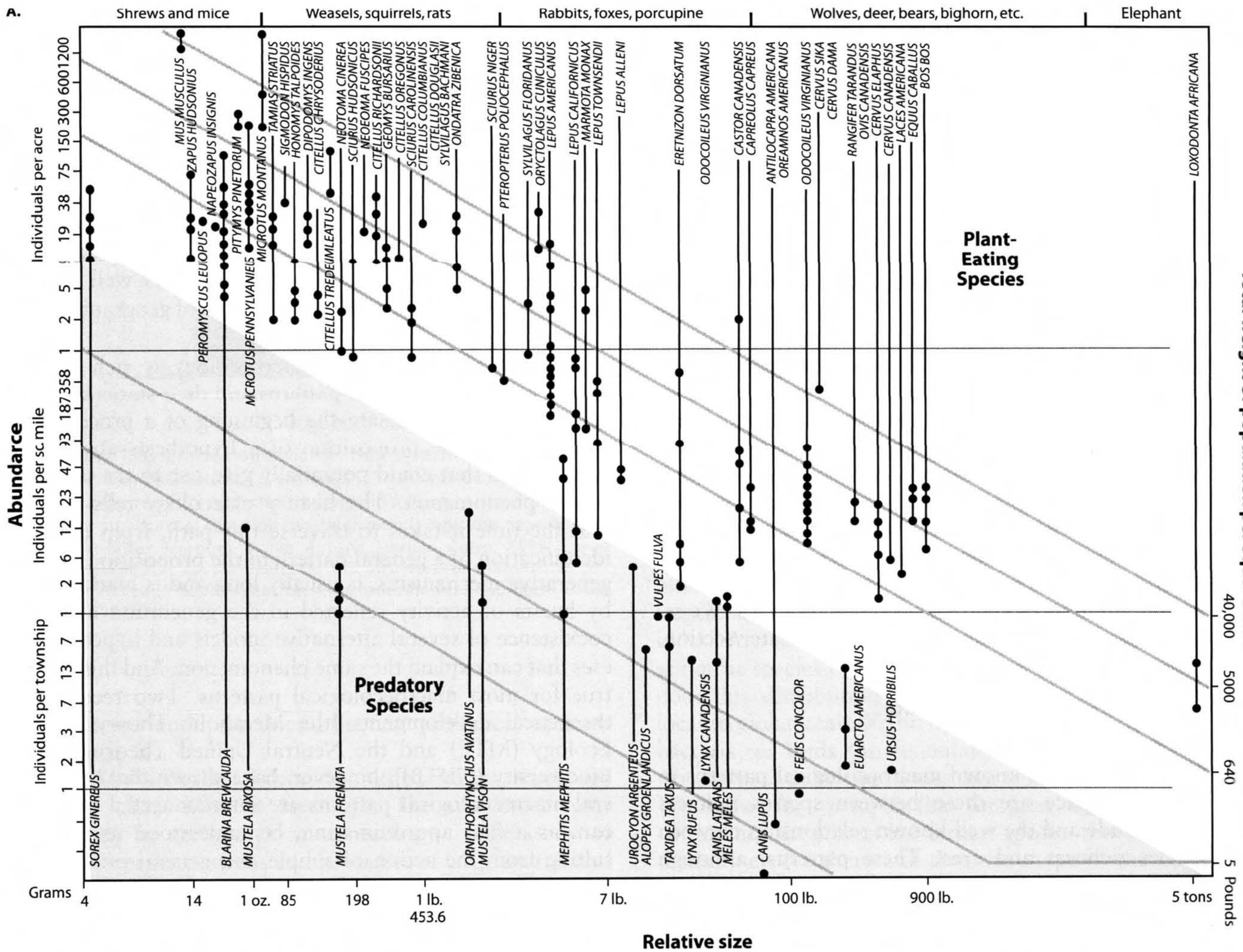

Figure 2. The relationship between population density and body size for (A) mammalian herbivore and carnivore species (from Mohr Carl O. 1940. Comparative populations of game, fur and other mammals. American Midland Naturalist 24: 581–584) and for (B) 307 species of mammalian primary consumers. (From Damuth, J. 1981 Population density and body size in mammals. Nature 290: 699–700)

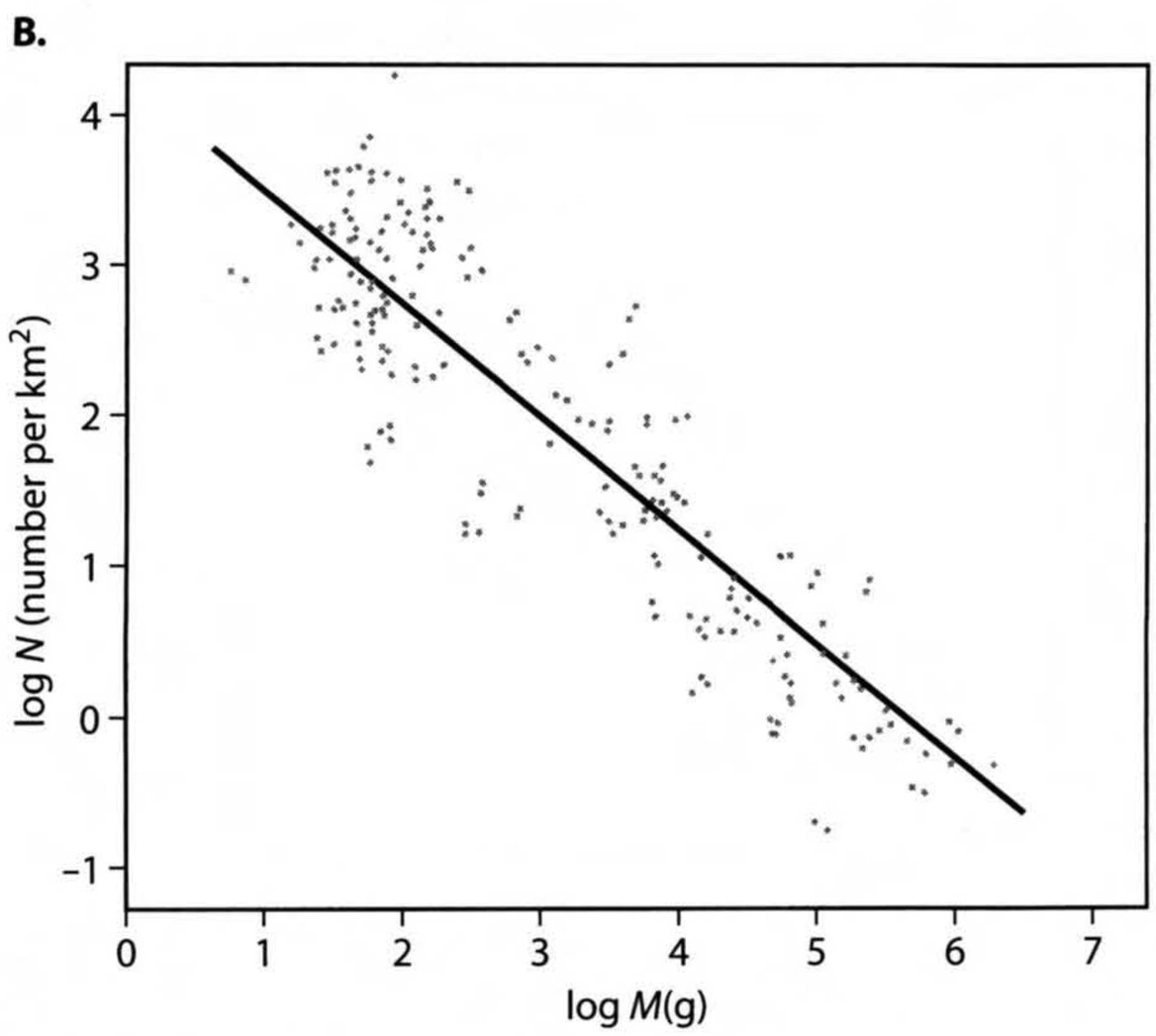

Figure 2. (*cont.*)

biotic forces in affecting diversity regulation. His reasoning was that one approach to assess the importance of biotic factors (such as competition and predation) was to compare empirical patterns against the results of a stochastic model that do not assume their existence. To do this, he used stochastic models first developed in the context of population genetics under neutrality. Twenty-five years later, in 2001, Stephen P Hubbell expanded this approach and developed what he originally called the unified neutral theory of biodiversity and biogeography, which is also known as neutral macroecology because it is capable of generating several of the patterns usually studied by macroecologists, such as species abundance and species–area relationships.

The quantitative nature and predictive potential of neutral macroecology facilitated the development of testable null hypotheses for macroecological patterns under the assumption that individuals are equivalent (neutral) in terms of their vital rates of death, birth, migration, and the probability of becoming a new species. In practice, neutral macroecology builds on the theory of insular biogeography proposed by MacArthur and Wilson in 1963 by assuming a source area of immigrants or metacommunity, which in the context of neutral theory represents a biogeographic unit within which most member species originate, live, and become extinct, and which in turn contains several local communities embedded in it. However, unlike island biogeography theory, it assumes that individuals, instead of species, are equivalent. This allows neutral macroecology theory to provide precise predictions of the shape of the distribution of species' relative abundance among other patterns.

In its current form, neutral macroecology applies to trophically similar species, which, in local communities,

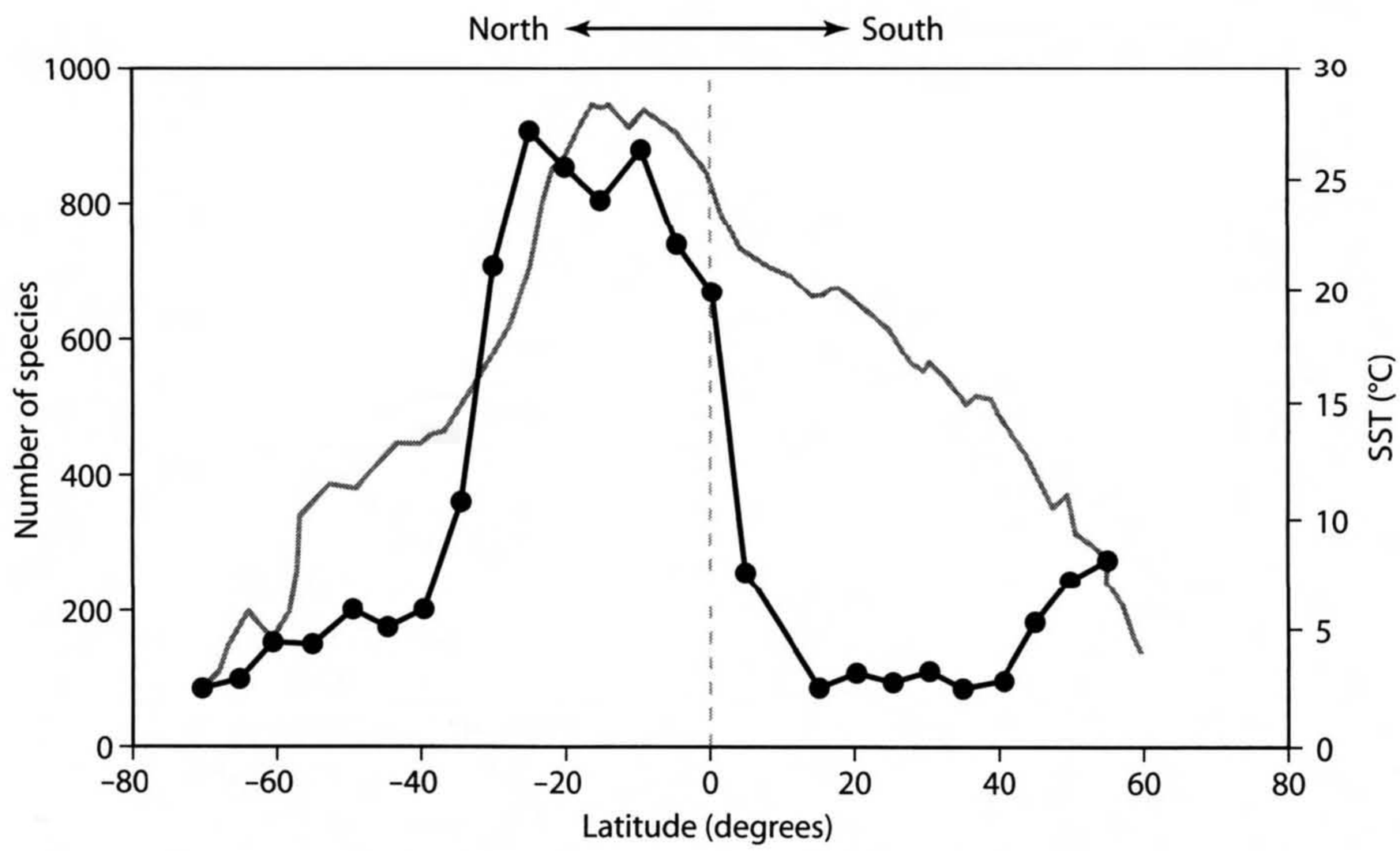

Figure 3. North–south view of the latitudinal diversity gradient of marine gastropod prosobranchs along the north- and southeastern Pacific shelves, from north Alaska to Cape Horn (gray line). Mean sea surface temperature (SST) along the continental margin is also shown (segmented line). (From Valdovinos, Claudio, Sergio A. Navarrete, and Pablo A. Marquet. 2003. Mollusk species diversity in the Southeastern Pacific: Why are there more species toward the south? Ecography 26: 139–144)

undergo random fluctuations in abundance, a process called ecological drift, as a consequence of stochastic birth, death, and immigration processes. Diversity in the local community is maintained by immigration from the metacommunity, where in addition to death and birth processes, speciation occurs. Thus, under neutral macroecology, community assembly is a process resulting from stochastic immigration only (i.e., dispersal-assembled communities) instead of resulting from adaptive divergence in species niches (i.e., niche-assembled communities). According to neutral macroecology, the relative species abundance distribution and the shape of the species–area relationship can take different forms, depending on the average rate of immigration from the metacommunity and the value of the so-called biodiversity number, $\theta = 2J_M v$, where J_M is the total number of individuals in the metacommunity and the speciation rate.

The dynamic, individual-based, quantitative and stochastic character of neutral macroecology theory and its ability to make predictions that can be compared to empirical patterns have led to its rapid development as a null hypothesis for macroecological patterns.

5. METABOLIC THEORY

Ever since Alfred Lotka, energy availability, acquisition, and apportionment have been thought to be essential for understanding biodiversity and ecosystem functioning. The metabolic theory of ecology provides a simple framework to analyze the role of energy flows from individuals to ecosystems. The core of metabolic theory rests on the understanding of individual metabolism and deriving its consequences for population, community, and ecosystem patterns and dynamics.

The efficiency with which energy is captured, delivered, and transformed by an organism for survival, growth, and reproduction is critical to individual fitness. This being the case, one might expect to find some general principles and regularities associated with energy acquisition and transformation. One such regularity, referred to as Kleiber's rule (after the Swiss physiologist Max Kleiber), describes how body size, M (mass in grams), is constrained by individual metabolic rate, B (watts, W), the total rate of energy transformation by an organism. This relationship is described by a simple mathematical function called a scaling law of the form

$$B = B_0 M^b, \tag{1}$$

where B_0 is a normalization constant independent of body size, and b is an "allometric" or scaling exponent. Kleiber was first to recognize that this scaling exponent takes a characteristic value of $b \approx \frac{3}{4}$. Despite the simplicity and ubiquity of Kleiber's rule, the mechanisms underlying it eluded biologists for more than 70 years.

A general, mechanistic explanation for Kleiber's rule was first proposed 1997 by Geoffrey West, Brian Enquist, and James H. Brown. The fundamental assumption of their model is that natural selection has resulted in the optimization of biological distribution networks in order to minimize the costs of transporting energy and materials within organisms. They demonstrate, theoretically, that the optimal solution to this problem is a hierarchical, fractal-like distribution network with space-filling geometry and size-invariant terminal metabolic units (e.g., mitochondria, chloroplasts). One of the consequences of these geometric constraints is the ¾ power exponent discovered by Kleiber. The model provides a parsimonious explanation for why a large number of functional and structural characteristics of organisms, which had been well known to ecologists and physiologists, such as growth rate, lifespan, and home range, relate to body size with scaling exponents that are simple multiples of ¼ and under which circumstances they might deviate from this theoretical expectation. The existence of such universal scaling laws implies that dynamically and organizationally, all mammals, for example, are on the average scaled manifestations of a single idealized mammal, whose properties are determined as a function of its size. That is, in terms of almost all biological rates, times, and internal structure, an elephant is approximately a blown-up gorilla, which is itself a blown-up mouse, all scaled in an appropriately nonlinear, predictable way This work paved the way to the MTE outlined in 2004 by James H. Brown and collaborators.

By explicitly focusing on the causes and consequences of individual metabolic rate, the MTE provides new opportunities to deal with the inherent complexity of ecological systems at different levels of biological organization. We exemplify this approach by showing how metabolic theory can be used to derive predictions on species abundance within communities, as derived by these authors.

Because the maintenance and reproduction of an individual require energy, everything else being equal, the maximum number of individuals per unit area, N, that a species can achieve will be proportional to the ratio of the rate of resource supply per unit area in the environment, R, and the individual metabolic rate, B

$$N \propto \frac{R}{B} \tag{2}$$

This expression leads to

$$N \propto M^{-\frac{3}{4}}. \quad (3)$$

Indeed, as we saw earlier, John Damuth had already reported in 1981 that the relationship between abundance and body size typically yields exponents of approximately $-\frac{3}{4}$, which has since been shown to hold across a wide variety of organisms from microbes to trees. Equation 3 also implies that that total energy flux by a population (i.e., $N \times M^{\frac{3}{4}}$) is independent of body size, meaning that species populations within communities are equivalent in the amount of energy that they control, the so-called Energetic Equivalence Rule. However, this relationship should hold for species using the same resource, which is not the case if we work with complete communities where species occupy different trophic positions and feed on different resources. To extend the theory to local communities of trophically dissimilar species, we need to consider that species occupying different trophic positions usually differ in size (e.g., predators are usually larger than their prey) and that the efficiency of energy transfer between trophic levels is usually low ($\sim 10\%$). Once these characteristics are taken into account, metabolic theory predicts that population density (N) across trophic levels should scale with mass as M^{-1} and that biomass (i.e., $N \times M$) should be independent of body mass, which happens to be a well-known pattern in aquatic ecosystems. Empirically, analyses of freshwater and marine communities across trophic levels agree with the expectations of metabolic theory

A novel contribution of MTE has been to derive a new expression that characterizes the combined effects of body size and temperature on metabolic rate:

$$B \approx b_0 M^{3/4} e^{-E/kT} \quad (4)$$

In statistical mechanics, the term $\exp(-E/kT)$, often referred to as the Boltzmann factor, is proportional to the fraction of molecules of a gas that attain an energy state of E at an absolute temperature T To react, the molecules must possess *activation energy*; that is, they must collide with one another with sufficient energy to change their state. Temperature increases the proportion of molecules that attain sufficient energy to react. Hence, the Boltzmann factor can be used to describe individual level biochemical kinetics and metabolic rate. Recent expansions of metabolic theory range from the analysis of the effects of body size and temperature on nucleotide substitutions, speciation rates, and the latitudinal diversity gradient to ecosystem respiration and the carbon cycle.

Macroecology likely represents a moment in the investigation of complex ecological systems, an attempt to come to terms with ecological complexity Much remains to be done to advance the macroecological research program and to cope with some of the criticisms against it. Macroecology needs more and better data of ecological systems and dynamics from local to regional, continental, and global scales. Although for many questions the reliance on published data sets and compilation studies will be inevitable, macroecology needs to back up some of its key empirical patterns and claims with experiments and field studies specially designed to assess them or to test their predictions. In addition to this, there are two exciting scientific paths whose developments are of paramount importance to macroecology The first is the need to better link reductionistic (microecological) with macroecological patterns and explanations. At the end of the day, fundamental principles and laws should also be at work no matter the scale of analyses and thus can help to design and interpret small-scale experiments involving few species or the response of ecosystems to human-driven perturbations. Notice that this is not a purely academic exercise. A general theory of ecological systems and dynamics will help to generate new and better management strategies and policies to ameliorate the impact of humans on ecosystems and to restore their functioning and the services they provide to humanity This link has not been sufficiently explored. The second is the daunting task to unify neutral macroecology and metabolic theory Energy and stochasticity are essential components of living systems from cells to ecosystems. Their unification in a stochastic theory of energy flow will be a great scientific achievement.

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