Integrating macroecology through a statistical mechanics of adaptive matter

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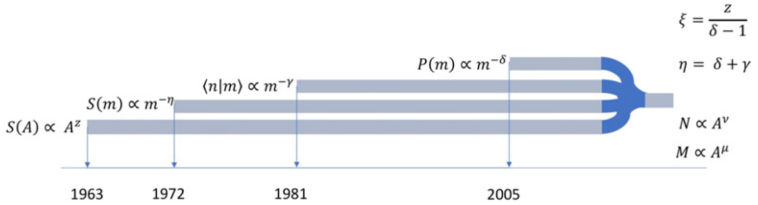

Fig. 1. Time line associated with the description of different macroecological patterns and their integration through statistical mechanic approaches, such as that proposed by Zaoli et al. (1): The species area relationship $S(A) \propto A^z$, the size spectra$S(m) \propto m^{-\eta}$, the scaling of density and size $\langle n|m \rangle \propto m^{-\gamma}$, and the power law distribution of body sizes $P(m) \propto m^{-\delta}$. At the far right are the relationships ξ, η among exponents derived by Zaoli et al. (1), as well as the prediction for the scaling of total biomass (M) and abundance (N). *A*, area; *m*, organismal mass; *n*, number of individuals; *S*, number of species.

Science advances through synthesis and integration by identifying common processes and principles from disparate observations and highlighting the unity underlying diversity. This process is exemplified by advancements in astronomy and physics in the 17th century, when Tycho Brahe's catalog of the positions of stars, moons, planets, and comets provided the empirical foundations for Kepler's laws of planetary motion and Newton's law of gravity. Brahe's natural history of the Universe led to a theory of nature that continues to shape our view of the natural world. Ecology seems poised at a transition like that of 17th century physics: the achievement of a general theory of biodiversity based on first principles. As shown by Zaoli et al. (1) in PNAS, one of the interesting aspects of this theory is that it looks a lot more like physics, particularly statistical mechanics, than classic ecology.

What Tycho Brahe did for astronomy in the 17th century, von Humboldt and other great explorers did for natural history and ecology in the 19th century, with the difference that a theory equivalent to Kepler's or Newton´s has not yet eventuated, and ecologists have remained fascinated with understanding the uniqueness of species, cataloging the varieties of organisms and studying their forms, functions, and interactions in ecological systems. Most may even think that the daunting complexity of ecological systems precludes the identification of general rules and thus the achievement even of an integrated theory, much less a unified one (e.g., ref. 2).

The efforts of these early naturalists, however, led to the principle of natural selection and its subsequent mathematical formalization, within the context of the neo-Darwinian synthesis of the 1930s. During this period, a large collection of idiosyncratic observations gave rise to a mathematical theory of evolution by natural selection, which serves as a cornerstone of modern biology. In hindsight, this progress may seem inevitable, but such an achievement was viewed by most at the time as highly improbable. For example, Osborn (1926, cited in Bennett's foreword to ref. 3) concluded that "The causes of 'variation,' to use the term [Darwin] used for the evolutionary process. . . may prove beyond human solution." History has proven Osborn wrong, as the evolutionary process rests on solid theoretical grounds, thanks to the architects of the evolutionary synthesis. The basic difficulty was, as Bennett said, a lack of understanding of the nature of biological variation. A similar process is happening in ecology and the difficulty is a lack of understanding of the main drivers of ecological variation and invariance. In other words, we need to identify the state variables of ecological systems and the observables deriving from them.

Early in the history of ecology, some regularities—or macroscopic patterns—became apparent in the form of probability distributions or as simple scaling relationships of power law form (4). Examples of these are: the relative species abundance and their size distribution (5–7); the change in the number of species with area or species area relationship (8); the relationship between metabolic rate and organismal mass (9), size, and area (10); and density and size (11, 12), among others (Fig. 1). These relationships usually showed constancy, or invariance, across time, space, and taxa, and became the basis of the subdiscipline of macroecology (13, 14), which emphasizes the existence of general patterns and the development of theories based on first principles (13, 15, 16) in a disciplinary background

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dominated by idiosyncratic explanations and phenomenological analyses. Early theoretical attempts to integrate macroecological patterns are represented by the seminal study of Preston (17), relating the species area relationship to the distribution of abundance, and later in the recognition of the existence of patterns in three dimensions, relating density, size, and number of species (18–20). More recently, however, the integration of patterns attracted the attention of physicists, which in interaction with theoretical ecologists, started to develop a quantitative framework to analyze the relationship among exponents characterizing several scaling patterns (21, 22). In PNAS, Zaoli et al. (1) expand and improve on these prior works, generating precise relationships among exponents (Fig. 1) and showing that they emerge from general stochastic models of community dynamics, where birth and death rates, as well as per capita growth, are a function of size and constrained by resource abundance. Interestingly, the relations among scaling exponents resemble the hyperscaling relationships associated to critical-phase transitions in physics (23). There is mounting evidence that critical phenomena are important in biology and ecology (24–27), and the discovery of ecological hyperscaling provides further support for it.

This theory is not alone in establishing the fundamental importance of area, number of individuals, number of species, and size as state variables, from which different ecological observables can be derived. Alongside it are two recent theories: the theory based on the maximum entropy principle—or MaxEnt (28–30)—and the Neutral Theory of Biodiversity (31). These theories, which are generating a paradigm shift in ecology, are rich in predictions and poor in adjustable parameters [i.e., efficient theories (16)] and are anchored in statistical mechanics (32), as is the approach of Zaoli et al. (1). Statistical mechanics is an approach that uses the theory of probability to study the macroscopic properties of systems composed of many interacting particles, which in the case of ecological systems correspond to individuals that have well-defined rates of birth, death, and resource use, and are able to establish a dialogue with their environment through niche construction. I call these particles adaptive matter. In this context, the new ecology that has been slowly emerging during this century represents a statistical mechanics of adaptive matter. However, unlike in physics, where thermodynamics preceded statistical mechanics, in ecology we have the statistical mechanics, but need a first-principles theory for the thermodynamics of adaptive matter with which to integrate it. This integration will likely come from the expansion of the Metabolic Theory of Ecology (33) that links the basic processes characterizing adaptive matter (i.e., reproduction, maintenance, and growth) to size and temperature. In particular, we need to achieve an integrated theory where: (*i*) the role of state variables and their scaling can be justified from first principles, as in West et al. (34); (*ii*) other ecologically important state variables (i.e., temperature) could be explicitly incorporated; and (*iii*) thermodynamic extremum principles (e.g., ref. 35), akin to the maximization of information entropy in MaxEnt, can be better linked into the theory. The integration of Neutral Theory, MaxEnt, and Metabolic Theory into coherent statistical mechanics and thermodynamics of adaptive matter is by far the largest challenge ahead, and an urgent one in the context of providing understanding of and solutions to the pressing environmental problems affecting our biosphere and the socio-ecological systems within it (16, 36). It is good to have theories for macroecological patterns, but not too many and not too late.

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