



# Statistical mechanics of complex ecological aggregates

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## Abstract

A fundamental limitation of classical science was its inability to explain how order could emerge out of uncertainty and indeterminism. The approach to solving this dilemma has been to develop theories of how properties of aggregated systems arise from the properties and interactions of their parts. The basic assumption of such ideas is that there is a tension between the tendency of an aggregated system to change and the constraints that are imposed upon that system by virtue of the behavior of and interactions among the parts. The balance between constraint and change gives rise to a hierarchy of aggregated structures that exhibit regular, repeatable attributes to the degree that constraints are able to maintain change across time within boundaries that define the nature of the structure. This basic view of causality in complex systems suggests an approach to defining a statistical mechanics for ecological systems that can be used to generate new theoretical descriptions of biological diversity. This approach is illustrated by introducing the idea of a “geographic population system” of a species and illustrating how change and constraints interact within this system to determine statistical properties such as geographic range size, and mean-variance scalings. The concept of a geographic population system is then used to develop alternative descriptions of the kinetics of biological diversity. Assuming that these alternatives are complementary, it is possible to develop a general description for biological diversity that shows how lower level change (geographical population dynamics of species) are constrained by the environment and genetic systems of species to determine rates of origination and extinction of taxa over long periods of time. © 2004 Elsevier B.V. All rights reserved.

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## 1. Introduction

Classical science was based on the assumption that nature worked according to fixed laws in a machine-like manner. The mechanical view of nature implied that if one knew all the laws of nature and the locations of every object contained in it, one could perfectly predict

what would happen in the future as well as construct a perfect description of the past. This thinking was applied to biology in the form of the natural theology of Paley. Organisms were viewed as being designed to fulfill specific roles in nature, and the whole of biological nature was organized into a series of more complicated designs with humans at the pinnacle, being the most perfectly organized of all species.

Thermodynamics forced upon science the realization that no machine was perfectly efficient. There-

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fore, it was not possible to perfectly reconstruct the past or predict the future from a single snapshot. More information was needed since events could not be specified with perfect precision. Thermodynamics required an “arrow of time” that pointed from the past to the future. Quantum physics introduced the notion that the universe contained a large degree of uncertainty that could never be removed, regardless of how much information one had about the state of the universe. Recent understanding of nonlinear systems, particularly those that exhibit chaos, reinforced the idea that perfect understanding of the past and the future was fundamentally impossible. These notions forced physicists to rethink how events occur in time and space. Rather than being a perfect machine, nature was seen to be full of uncertainty, unpredictability, and contingency. Despite this, order is found in abundance in nature at all levels, from physical to biological. This is because physical and biological laws are probabilistic, and emerge only at certain scales and under certain conditions.

In ecology, the first theoretical constructs used to describe ecological systems were based on the same kind of models used in classical science. Rather than being probabilistic, these models were completely deterministic. They proved to be of limited utility because ecological systems are full of uncertainty, unpredictability, and contingency. This left some ecologists claiming that ecology is devoid of laws (e.g., Peters, 1991). The absence of ecological laws, however, is due to the fact the ecologists have failed to apply appropriate techniques to elucidate any laws that might exist.

The approach needed to discover ecological laws, if they exist, requires the recognition that ecological systems are complex, aggregated systems, that is, they are composed of many interacting parts. Such systems are not devoid of order, in fact simply being aggregated implies a kind of hierarchical order exists. It turns out that all physical systems are also complex, aggregated systems, and many of these demonstrate exceedingly law-like behavior. Seventy five years ago, Lotka (1925) suggested that complex biological aggregates could be described using a generalized version of statistical mechanics. In this chapter, I explore Lotka’s suggestion further by considering how complex aggregated systems develop order, then applying these insights to develop a statistical

mechanics useful for analyzing geographical populations of species and the evolution of biological diversity.

## 2. The nature of aggregated systems

The basic premise that I assume to underlie any description of a system as an aggregate of smaller systems is that there are two fundamental influences on aggregate behavior, namely (1) energy flows within and across the aggregate’s boundaries, and (2) constraints on the possible configurations that those energy flows can impose upon the aggregate. From these two influences, aggregate behaviors arise that converge on a gradient of possible outcomes, each dependent upon the relative balance between energy flux and constraint. At one end the spectrum are simple outcomes that can be catalogued and described with relative ease. Such systems are dominated by constraint. At the other end are outcomes so complex that no human mind can possibly comprehend them. These systems are dominated by energy flux and change.

In order to understand complexity, one needs to begin with some assumptions regarding how nature is, in fact, put together. These assumptions eventually, with the collection of enough data, give rise to theories, and eventually for some phenomena, laws. Assumptions, theories, and laws, however, are all ultimately constructions of human minds. What matters is not whether these constructs are “true” or not, but whether they are “useful” (Geise, 1998). I begin with what I believe is a somewhat general description of how an aggregated system *ought* to work. This description lays out what I take as a set of fundamental assumptions about nature.

How does the behavior of an aggregated system arise from the interaction of the energy imparted to it by the collective motions of the parts that make it up and the constraints that operate to restrict those motions? The existence of movements of the parts of an aggregated system implies that there will be changes in aggregate behavior. That is, systems are assumed to be in a constant state of change, albeit on different time scales, and these changes will continue until the universe (or a subset of it) attains a state of maximum entropy. Constraints are imposed on energy flows in systems by a variety of mechanisms.

Ultimately, constraints are imposed on all physical systems by the four fundamental forces of gravity, electromagnetism, and the strong and weak nuclear forces and by the laws of thermodynamics. More proximately, there are constraints that arise from the spatial configuration and interactions among system components and from interactions of system components with physical structures that are not part of the system.

Matter in the universe is not uniformly distributed, if so, there would be no aggregates of different sizes for scientists to study. Rather, matter clumps together at different spatial and temporal scales. The gross structure of these scales can be seen in the distribution of different sized “particles” in the universe (Fig. 1(A)). At the size scale of the biological world, there are a diversity of sizes of living systems as well, but the organization within and diversity among them is apparently much more complex (Fig. 1(B)). Thus, the universe as we know it can be defined by two axes: one axis defines the range of sizes of different aggregates, the second axis defines the range of complexity of aggregates of a given size (Barrow, 1998). The complexity axis describes simple physical systems at one end and most biological systems (including systems created by humans) at the other. Biological complexity, at least on the surface, seems to a very different kind of complexity than exists in non-biological systems. This is most evident in our own species, where the processes of biological evolution have generated perhaps the most complex system of all: the human brain and its products. Despite appearances, there is a great deal in common with the mechanisms that generate order in complex systems, both biological and non-biological.

### 3. Emergence of order in complex systems

At the scale of quantum systems, we are faced with the apparent paradox that there is a large degree of uncertainty in the behavior of elementary particles, yet they often form highly stable aggregates such as atoms, molecules, crystals, etc. This paradox has given rise to the famous “measurement problem”, debated by Einstein and Schrödinger (Lazyer, 1980; Nadeau and Kafatos, 1999). The problem arises because the properties of a particular particle, say a photon, are

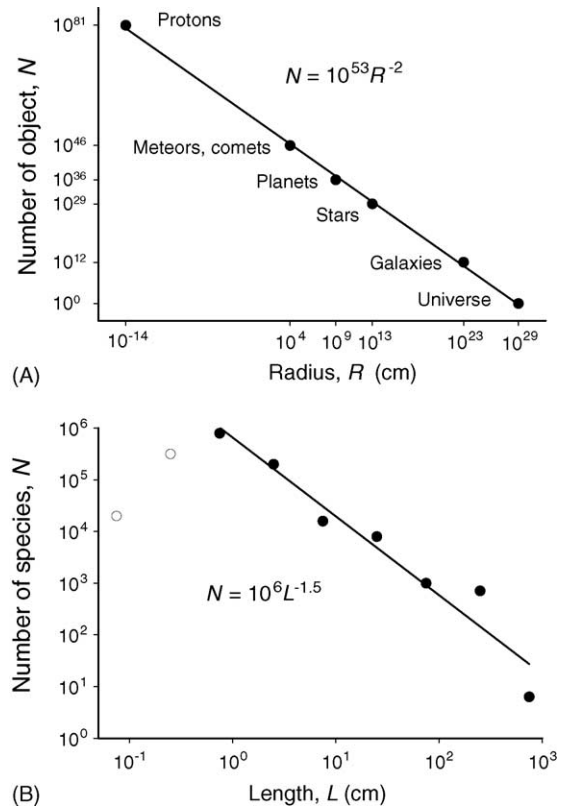


Fig. 1. (A) Approximate numbers of aggregated objects in the universe as a function of their radius. (B) Approximate numbers of species of multicellular animals as a function of size, based on May (1978) data. Open circles represent data for the two smallest size classes that were not included in the calculation of the power law. Note that data are plotted on the same scale as in A. Numbers of species of smaller organisms used to calculate the power law are very likely to be underestimates (May, 1988), so that the exponent of the power law is most likely much higher.

probabilistic. A photon can occupy more than one state, but it is uncertain which of those states the particle occupies. However, when the particle is measured, it is found to be in a specific state. This implies that the measurement determines the actual state that the particle occupies. Einstein argued unsuccessfully that the probabilistic nature of particles was actually due to a lack of information, rather than a fundamental uncertainty in the way the particle behaves. According to Einstein, any given particle really exhibits deterministic behavior, but we do not discover that behavior until the particle is measured. The alternative to Einstein’s position is that the

uncertainty of a particle's behavior is an irreducible quality of the particle until a measurement is made. If measurements of particles determine their actual states, then it follows that all macroscopic states are indeterminate until an observer is present to measure them. This is highly unsatisfactory if science is supposed to be an objective, observer-independent activity.

A variety of solutions to the measurement problem have been suggested. Among these, Layzer (1990) interpretation provides perhaps the most relevant approach upon which to build an understanding of ecological complexity. Layzer (1990) argued for what he called the Strong Cosmological Principle. The principle states that a complete description of the universe can only contain statistical information. The term "statistical information" as used by Layzer, means that the properties of everything in the universe are probabilistic. The probabilities define the nature of the universe as a whole, and not the properties of any particular subsystem we happen to measure. We obtain a particular value for a measurement of a specific subsystem in proportion to the relative frequencies of possible values for measurements taken on an infinite number of subsystems identical to the one we happened to measure. What does it mean when we obtain the same value for a measurement over and over again? It means that the relative frequency of that value in the universe is close enough to one that there is a minuscule chance of obtaining any other value. We can never be absolutely certain that the same value will always be obtained, because the properties of the universe that determine the value we obtain are probabilistic.

Given this underlying probabilistic structure of the universe, what implications does it have for understanding how order emerges in kind of complex systems envisioned in the previous section? The most important consequence is that the constraints imposed on any complex system cannot be absolute, but must probabilistic. This means that the effects and strength of those constraints must vary from system to system, and will also vary across space and time in the same system. This variation will ensure the individuality of each complex system. If this is true, then how do regularities or laws develop? The behavior of classical physical systems, in particular, appears to be highly regular and repeatable. If each system is unique, why

should we expect the laws of classical physics to explain anything? For example, a planet is a complex aggregate of a large number of particles each with indeterminate behavior. Why should Newton's law of gravity apply to its motion around a star?

The answer has to do with the structure of the probability distributions underlying constraints on systems. Constraints vary in their "strength" from system to system. Strong constraints have high relative frequencies, that is, systems experiencing such constraints almost always behave the same way. Weak constraints have probability distributions that allow for a relatively large number of possible behaviors. With respect to constraints, orderly behavior arises in two ways, corresponding to what Schrödinger (1944) referred to as "order from disorder" and "order from order". Order arises from disorder in systems with weak constraints. Order arises from order in systems experiencing strong constraints.

Any description of a complex system begins by defining what the components are that comprise the system. Aggregates are often referred to as a macroscopic entities, while the components are called microscopic entities. The states of both macroscopic and microscopic entities are determined by the structure of the statistical distributions that describe the range and relative frequencies of states that each entity can occupy. The state that each microscopic entity occupies is described by a variable, and the collection of microscopic variables will behave according to a probability distribution that describes the likelihood of each variable occupying any particular state. Likewise, the states occupied by macroscopic entities can be represented by a smaller number of macroscopic variables, each of which is associated with a probability distribution derived from the probabilistic behavior of the microscopic variables.

Order from disorder can only arise in systems where the scale of microstates is vastly smaller than the scale of macrostates. When this is true, the contribution of each microstate variable to the behavior of each macrostate variable is extremely small. Spatial variation in microstate variables will have little influence on the behavior of macrostate variables, and temporal kinetics of microscopic variables will be resolved so rapidly that they do not impact macrostate kinetics. The tiny impact of any one microstate variable on aggregate behavior in a

sense “decouples” microscale fluctuations from macrostate behavior. Imposing relatively mild constraints on the behavior of microstate variables will lead to a sufficient amount of correlation among them to ensure macrostate behavior that appears “deterministic”. Deterministic behavior in this sense means spatially and temporally consistent behavior of macrostate variables. In such systems, “cause” and “effect” relationships can exist among macrostate variables because changes in behavior in one macrostate variable will always (that is, with relative frequency approaching one) produce the same effect on other macrostate variables. Note that the *mechanism* of these causes and effects may reside in complex interactions among a vast number of microstate variables. The number of microstate interactions may be so large that it is impossible to establish causes and effects among microstate variables. Systems typified by large differences in micro and macro scales are *large number systems* that have law-like macroscopic behavior. The fact that quantum uncertainties occur on scales vastly smaller than the macrostate variables that form the basic structure of classical physics allows for the existence of classical mechanics where macroscopic aggregations of matter can be described by precise, deterministic laws.

When the difference between micro and macro scales are relatively small, deterministic behavior of an aggregate may still arise if strong constraints govern the kinetics of microscale variables. In such systems, order arises because the constraints themselves are ordered. Strong constraints induce “coordinated” behavior among microscale variables, that is, all microstate variables behave in the same way because there are a limited number of “choices” available by virtue of the constraints. Strong constraints may be imposed upon the system from within or without. Internal constraints arise when the behavior of microstate variables is determined by strong correlations among the attributes they possess (i.e., from correlations among *micro*-microstate variables). External constraints are imposed upon microscale variables by the existence of interactions of microscopic entities with entities not contained within the macroscopic entities.

When micro and macro scales differ by relatively few orders of magnitude and constraints on microstate behavior are relatively relaxed, it is difficult to

establish clear deterministic patterns of cause-effect relationships at either the macro or micro scales. Systems like this are often called *middle number systems* (Allen and Starr, 1982). Descriptions of behavior in such systems often include “stochastic effects” at either the macroscopic or microscopic scales, or sometimes both. These stochastic effects can be thought of as relatively simple mathematical functions that summarize irrelevant complexity. The decision about what complexity is relevant is often arbitrary and may be made for a number of reasons. Often, there may be several alternative descriptions for the behavior of the system that differ in the amount of detail and the weighting assigned to different microstate variables.

The fact that multiple descriptions of a middle number might exist offers a unique opportunity to develop a more complete understanding of a complex system by assuming that each description is “true”. That is, different descriptions of the system can be viewed as complementary. By seeking commonalities among complementary descriptions of complex systems, a more complete understanding of such systems might arise. In what follows, I apply this principle of complementarity to the problem of the evolution of biological diversity.

#### 4. Statistical mechanics of ecological aggregates

The systems studied by ecologists are often complex aggregates that operate as loosely-constrained middle number systems. Ecologists must contend with fundamental problems of system identification since arbitrary decisions must often be made about how to define system boundaries. Because of this, there is a tendency for ecologists to proliferate hypotheses specific to individual, locally-defined “pseudo-systems” (i.e., the system being studied has no recognizable boundaries other than those imposed upon it by the observer). This has led a number of ecologists to seek more objective criteria by which to recognize system boundaries (Allen and Starr, 1982; O’Neill et al., 1986; Li, 2000). Aggregation is one way to establish “natural” boundaries: one simply adds up sufficient number of organisms or species until one has a large enough collection to exhaust the range of possible boundaries (Brown and



Maurer, 1989; Brown, 1995; Maurer, 1999). Once such an aggregate is formed (conceptually), then the problem is to define macroscopic properties of the aggregates that provide a framework for causal explanations (e.g., Brown and Maurer, 1987, 1989; Maurer and Brown, 1988; Li, 2000, 2002).

Here I examine the evolution of biological diversity from the viewpoint that evolving lineages of species are aggregates of individual organisms that exist within geographically restricted regions. Here, the microsystem describes the behavior of individual organisms, and the macrosystem describes the behavior of large collections of genealogically related species. I describe the statistical mechanics that relate microsystem behaviors to macrosystem properties. I begin with assumptions regarding the flows of energy through organisms and the constraints that act on those flows. From these assumptions, I show how the macroscopic description of the aggregated system is related conceptually to the constraints inherent in the system and its environment. I begin describing the geographical population system of an individual species, then show how this description is related to the description of the evolving species assemblage to which it belongs.

#### 4.1. *Geographical population systems*

For most plants and animals, it is relatively straightforward to recognize individual species (though there are many subtleties and complexities in defining species boundaries). It is often even more straightforward to identify the individual organisms that comprise a species (though again there are some important complexities for certain kinds of species). The sum total of all individuals belonging to a single species that are alive at a given time defines an aggregate system that has relatively discrete, recognizable spatial boundaries. These spatial boundaries form the *geographic range* of the species, and the sum total of all individuals within that range comprise the *geographical population system* of the species. Are the properties of such an aggregate law-like in any empirically meaningful sense?

To derive a law-like description of the total population of a species of plant or animal, we must deal with the spatial context in which that population exists. For a given species, individual organisms live

in an environment that shows considerable spatial heterogeneity. Brown (1984) first proposed that the variability in this environment must be spatially autocorrelated, so that places close to one another tend to have similar conditions. Initially, we will assume that individual organisms within a species are more or less identical with respect to their ability to tolerate these environmental conditions. If this is true, then there must be a small number of sets of conditions that provide the best environment for individuals. Since the environment is spatially autocorrelated, there will be a few regions that provide the best conditions, and as one travels away from the spatial locations containing those conditions, the environment deteriorates with respect to the ecological requirements of the species.

The spatial context in which a species exists, then, provides a set of constraints on energy use by individual organisms by constraining the abundance and availability of appropriate energy sources and habitat conditions. The rest of the necessary constraints needed to derive a statistical mechanics for the aggregate come from the properties of the individual organisms. Each organism represents a specific realization of a set of genes in its cells. The genes possessed by an organism are often thought of as originating from a large “gene pool” that represents the total number of genes that exist within the species. Although the combination of genetic information in each individual is unique, the packaging of genes on chromosomes and the associated biochemical machinery determining how that information is assembled on new chromosomes during reproduction strongly constrains the possible combinations of genes that can be realized in any organism within a species. In addition, constraints on gene expression operate as the genetic program on the chromosomes is implemented to build an organism over its life cycle. Given these two sources of external (spatial context) and internal (genetic and developmental) constraints, how do they shape the flow of energy through the geographical population to lead to law-like macroscopic properties?

Energy enters into a geographical population system as individual organisms consume resources in the environment. The energy thus obtained is partitioned among two general processes. In multicellular plants and animals, the first process is the use of energy to build and maintain tissues and organ systems. The set of energy transformations that

underlie tissue accumulation and metabolism is vast and complex. Consequently, a large fraction of the energy diverted to these transformations is lost. Eventually, the organism is unable to maintain the complexly organized networks of energy transformations. Ultimately, the networks collapse and the organism dies. The timing of this death is determined by the external and internal constraints operating on the individual given its spatial location within the geographic range of the species. The other process to which ingested energy is allocated is the production of new, genetically similar copies of the organism. Again, the networks of energy flows are complex (especially in sexual organisms), but the end product of the second process is the birth of one or more individuals and their survival to reproductive age. The birth–death process that is the end product of energy flows through organisms has a negative feedback component such that as more organisms are encountered during the lifetime of an organism, the lower the net output of its birth–death process (the strength of this density-dependent feedback varies considerably from species to species).

Thus, the flow of energy through a geographical population leads to a spatially varying, density dependent birth–death process. The spatial boundaries of the geographical population are determined by the set of environmental conditions where the average output of the birth–death process is less than or equal to zero. Note that by this definition, the aggregate (geographical population) has properties that are spatially and temporally averaged. At any given point in space and time the individual organisms observed will be found in a discrete set of conditions defined by their immediate nutritional state and point within their life cycle. When sets of organisms are aggregated over space and time, statistical populations are formed that can be described by rates of birth and death. The dynamics of the geographical population are determined by long-term patterns in these rates and the degree to which they are spatially autocorrelated across the geographic range.

Does the geographic population of a species act as a single system or only as a haphazard collection of individual populations? There are at least two major processes that connect local populations together to form aggregated geographic populations. First, the process of migration among local populations can

potentially correlate the dynamics among individual populations. The degree to which this occurs depends on the adaptations for dispersal that individual organisms possess and on any environmental barriers to migration. At one extreme, there might be complete panmixis so that a single description might be used to characterize the entire geographic population of the species. At the other extreme, individual local populations might be completely isolated from all other populations so that each population would require a single description. Most geographic populations will fall somewhere in between these extremes, so that a migration component is needed to describe the dynamics of each local population. Migration is often most important in the description of geographical population dynamics when the population is moving spatially, such as when a species is spreading across a newly colonized landscape (Lele et al., 1999).

A second major process that can integrate dynamics of local populations into a geographical population is geographic variation in population vital rates (Pulliam, 2000; Maurer and Taper, 2002). The origin of this variation lies in the fact that the genetically determined attributes of organisms in a species are limited to a relatively small set of environmental conditions in which they can produce energy for survival and reproduction. Since the environment in which these organisms exist is spatially autocorrelated, it follows that locations where the species can maintain viable populations will be clustered together in geographic space (Brown, 1984; Maurer, 1999). Geographic patterns in population vital rates reflect this clustering (Maurer and Taper, 2002). For example, for some species, stable geographic range boundaries may arise because populations at the range boundary have low resilience and high intraspecific competition (Maurer and Taper, 2002).

Geographic ranges can be considered to be macroscopic systems because the dynamics of populations within the range are coordinated by both internal constraints (adaptations of individuals within populations) and external constraints (geographic variation in environmental conditions). A number of macroscopic attributes of geographic ranges arise from this coordination. Geographic range size, shape, orientation and location are statistical attributes of geographic ranges that vary among closely related

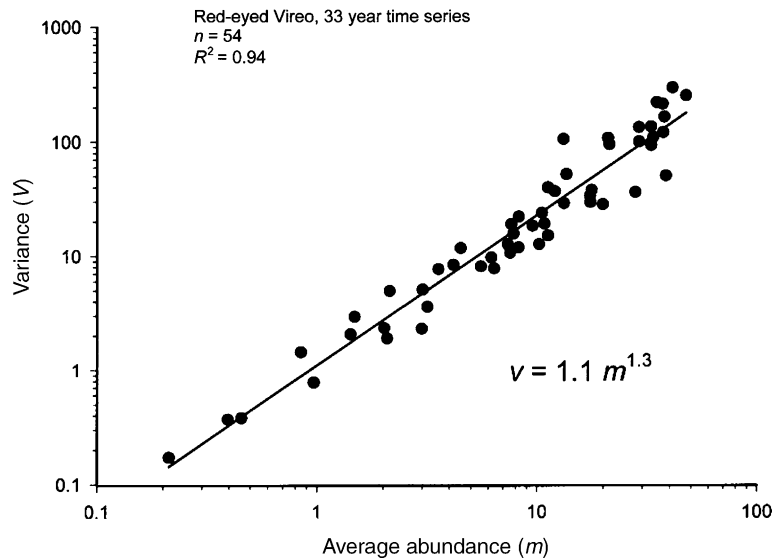


Fig. 2. A typical power law describing the relationship between variances and means of local population abundance for the red-eyed Vireo (Aves, *Vireo olivaceus*). Data were obtained from standardized censuses of the species during the breeding season conducted over 33 years (see Maurer and Taper, 2002 for details). Only censuses spanning the entire census period were used. This relationship is typical of those found for most animal populations (Taylor, 1961).

species (Maurer, 1994). Each of these attributes result from coordinated population dynamics across the range of a species. Statistical power laws relating means and variances of populations across the geographic range of a species (Fig. 2) result from geographic variation in population processes (Maurer and Taper, 2002; G.M. Nessler, personal communication). These power laws indicate how geographic variation in population processes leads to the formation of range boundaries (Maurer and Taper, 2002).

#### 4.2. A statistical mechanics for the evolution of biological diversity

In the last section, we saw how energy flows through geographical population systems are constrained by environmental and genetic properties of individual organisms so that the geographical population develops statistical attributes that describe its spatial distribution in terms of constraints on local population behavior. These constraints apply as long as there is no significant change in the genetical or environmental properties of the geographical population system. Short term environmental or genetic

fluctuations may not change the system, but over evolutionary time scales, we know that both environments and gene pools change substantially. When examining the fossil record, it is clear that species with new genetic properties appear from time to time and that species existing at one time period eventually become extinct. Ensembles of related species, referred to as clades, undergo a birth–death process on evolutionary time scales. This speciation–extinction process must be the cumulative outcome of changes in geographical population systems of different species. Shifting environmental conditions that result from long term patterns of climate change will change the constraints that operate on collections of different geographical populations. Some of this change is purely ecological (e.g., shifts in range boundaries) and some must involve changes in genetic information (e.g., speciation).

In this section I examine the evolution of biological diversity from a statistical mechanical viewpoint. The macroscopic description is obtained by modeling the additions and deletions of species as viewed from the fossil record. The microscopic description is developed from the dynamics of geographical populations as they change over evolutionary time. The parameters



of the macroscopic model of diversification are shown to be averages across species of the processes of evolutionary change within and among geographical populations.

4.2.1. Macroscopic model of diversification

Envision the number of species in a geographic region at a given point in time,  $t$ , as a list of species drawn from a species pool of size  $S_{\max}$ . Let the  $i$ th species in the pool be represented by a binary variable  $X_i(t)$ , where  $X_i(t) = 1$  if the species is present at time  $t$ , and  $X_i(t) = 0$  otherwise, where  $i = 1, 2, \dots, S_{\max}$ . Species  $i$  is present at time  $t$  with probability  $p_i$ . The number of species present at time  $t$  is  $S(t) = \sum_i X_i(t)$ , and the expected value of  $S(t)$  is  $E[S(t)] = S = \sum_i p_i$ . Thus, the rate of change in average number of species over time can be written as:

$$\frac{dS}{dt} = \sum_{i=1}^{S_{\max}} \frac{dp_i}{dt} \tag{1}$$

Four processes determine the presence or absence of a species, and therefore  $p_i$ : (1) a species will be present at time  $t$  if it has originated by speciation with probability  $\zeta_i dt$ ; (2) it may invade the region with probability  $\iota_i dt$ ; (3) it may become locally extirpated within the region with probability  $\varepsilon_i dt$ ; and (4) it may become extinct globally with probability  $\xi_i dt$ . The instantaneous rate of species  $i$  being added to the biota is  $\lambda_i dt = \zeta_i dt + \iota_i dt$ , and the instantaneous rate of species being deleted is  $\mu_i dt = \varepsilon_i dt + \xi_i dt$ . Thus, we have  $dp_i = \lambda_i dt - \mu_i dt$ . The average instantaneous rate of additions across species is  $\lambda dt = \sum(\lambda_i dt)/S$ , and the average instantaneous rate of deletions is  $\mu dt = \sum(\mu_i dt)/S$ . Therefore, the rate of change in average species number becomes

$$\frac{dS}{dt} = S(\lambda - \mu) \tag{2}$$

Typically, the instantaneous rates of additions and deletions for any given species are assumed to depend on the number of species present (Sepkoski, 1978, 1979, 1984; Walker, 1985; Maurer, 1989, 1999; Alroy, 1998; Maurer and Nott, 1998). If this species-richness dependence is slight or nonexistent, then  $S$  increases or decreases exponentially (Stanley, 1979; Raup, 1985). Eq. (2) is a macroscopic description of the kinetics of the average number of species. It can be parameterized with data from the fossil record (Sepkoski, 1978,

1979, 1984; Alroy, 1998). The important result that emerges from Eq. (2) is that the species richness of a clade depends on the difference in the per capita rates of additions and deletions (Maurer, 1989, 1999; Alroy, 1998; Maurer and Nott, 1998).

4.2.2. Microscopic model: ecological processes

In order to model the dynamics of species richness, one must define what one means by species. Initially, assume that species are discrete entities comprised of genetically related individuals who are reproductively isolated from individuals in other species. Further, assume that the geographic population of a species is composed of a large number of ecologically equivalent individuals. These two assumptions allow us to emphasize the role that ecological processes affecting population dynamics play in the diversification process. Later, the model will be expanded to examine populations composed of a number of different subpopulations that interact with the environment in different ways.

Assume that on a continent at a given point of time,  $t$ , there are sufficient resources to support  $N(t)$  individuals. The abundance of species  $i$  at time  $t$  is  $N_i(t)$ , and  $N(t) = \sum N_i(t)$ . Note that some species will have zero abundance. As before, let each species be represented by a binary variable  $X_i(t)$ , where  $X_i(t) = 1$  if  $N_i(t) > 0$ , and  $X_i(t) = 0$  if  $N_i(t) = 0$ . The presence or absence of a species can be considered to depend on its own abundance and, since we have the constraint  $N(t) = \sum N_i(t)$ , on the abundances of other species as well. The average number of species is, as before,  $S = \sum p_i(t)$  but now we assume explicitly that the probability of a species being present at time  $t$  depends on abundances of other species, so  $p_i = f_i(\mathbf{N})$ , where  $\mathbf{N}$  is a vector of the total abundances of all species. Thus, by the chain rule, Eq. (1) becomes

$$\frac{dS}{dt} = \sum_{i=1}^{S_{\max}} \sum_{j=1}^{S_{\max}} \frac{\partial p_i}{\partial N_j} \frac{dN_j}{dt} \tag{3}$$

Eq. (3) represents a microscopic description of the kinetics of average number of species. The partial derivatives connect processes occurring over ecological time scales (population dynamics of individual species across their entire range) with processes occurring over evolutionary time scales (additions and deletions of species).

To understand how the dynamics of geographical population abundance might affect additions and deletions of species, we require some idea of how total population abundances change over time. We assume that the population abundance of species  $j$  is a function of abundances of all other species in the clade. At each point within the geographic range of a species, there is a changing population *density*. Let  $\mathbf{x}$  represent a location within the geographic range, then population density of species  $j$  at that point is  $n_j(\mathbf{x}, \mathbf{n}, t)$ , where  $\mathbf{n}$  is the vector of species *densities* at location  $\mathbf{x}$ . If  $A_j(\mathbf{N}, t)$  represents the area of the geographic range of species  $j$ , then the kinetics of abundance of species  $j$  is

$$\frac{dN_j}{dt} = \frac{d}{dt} \int_0^{A_j(\mathbf{N}, t)} n_j(\mathbf{x}, \mathbf{n}, t) d\mathbf{x} \quad (4)$$

Note that the integral sums local population densities across the geographic range of the species. Note also that the size of the range is assumed to be affected by the abundances of other species in the clade. From Eq. (4), it follows that there are two sets of ecological processes that determine the rate of change in abundance: (1) local population dynamics that change densities at different locations within the geographic range ( $dn_j/dt$ ); and (2) dispersal dynamics that change the size and spatial configuration of the geographic range of a species ( $dA_j/dt$ ). Obviously, these two sets of processes interact. There will be diffusion of individuals among local sites, and if many individuals are produced in excess, the size of the range might increase as these individuals disperse into previously unoccupied geographic regions. Furthermore, when ecological conditions are severe, population density will drop to zero in regions previously occupied by the species, shrinking the size of the geographic range. The patterns of population density of interacting species will modify the kinetics of population abundance by providing resistance (or facilitation) to dispersal, and by limiting the population density within local sites.

The model outlined above is sufficiently complex that developing specific functional forms for abundance kinetics will present a great challenge. There have been a few studies that have attempted to estimate abundance kinetics for species invading new geographic regions (van den Bosch et al., 1992; Veit and Lewis, 1996; Lele et al., 1999), but these are not

sufficient to understand the role a species plays in diversity dynamics.

#### 4.2.3. Microscopic model: genetic processes

Consider now a population that is composed of a number of distinct *ecotypes*. Each ecotype is composed of a set of genetically related individuals that interact with the environment in the same way and share the same genetic history. Empirically, these ecotypes can be recognized by a characteristic aspect of their genome, such as a haplotype. At time  $t$ , we assume that there are  $G_j(t)$  such ecotypes in species  $j$ . The population density of the  $k$ th ecotype in all populations within the geographic range is  $n_{jk}(t)$ . Thus, the population density in Eq. (4) becomes  $n_j(t) = \sum_k n_{jk}(t)$ ,  $k = 1, 2, \dots, G_j(t)$ . Essentially the same kind of dynamics envisioned for species above can be applied to the dynamics in the number of ecotypes. Thus, we assume that there is a maximum number of ecotypes that can be generated by a species, say  $G_{j\max}$ . Then the number of ecotypes at time  $t$  can be represented by the sum of a set of binary variables  $Y_{jk}(t)$ , where  $Y_{jk}(t) = 1$  if  $n_{jk}(t) > 0$ , and  $Y_{jk}(t) = 0$  otherwise. The probability of the  $k$ th ecotype appearing in the population at time  $t$  is  $p_{jk}(t)$ . The average number of ecotypes is then  $E[G_j(t)] = G_j = \sum_k p_{jk}(t)$ , so the dynamics of the average number of ecotypes can be written as:

$$\frac{dG_j}{dt} = \sum_k \frac{dp_{jk}}{dt} \quad (5)$$

Several processes influence the additions and deletions of ecotypes. Additions occur by genetic processes of mutation and recombination, and by gene flow among populations. Deletions occur when an ecotype goes extinct globally or is locally extirpated. These processes depend on the spatial distribution of ecotypes across the geographic range of a species. There are two extremes along a continuum of possibilities. At one extreme, each ecotype is spatially isolated from all other ecotypes, and migration among ecotypes is rare. Thus, each ecotype forms a distinct subpopulation that undergoes its own population dynamics, and genetically represents spatially a distinct *deme*. These demes can diverge genetically by selection and drift if gene flow is low enough. Demographically, each deme will generally have a small population size, and thus will persist over a

shorter period of ecological time than the entire population. This extreme is a *Wrightian* population structure. At the other extreme, ecotypes will be widely distributed and may exchange genes to a certain degree. If the panmixis is complete and the species is sexual and outcrossing, then each individual represents a unique ecotype. This extreme is a *Fisherian* population structure. Any real species will have a population structure in between these extremes. The degree to which a species maintains either a *Wrightian* or *Fisherian* population structure will have a profound influence on the dynamics of ecotypes over time.

When there is significant genetic structure to the geographic range, then the dynamics of species richness will be determined by the complex demography of the ecotypes of each species as they interact with the environment and with each other. The dynamics of the geographic population of each species is determined by both the spatial and genetic structure of their respective geographical populations. The dynamics of average species number over time then becomes

$$\frac{dS}{dt} = \sum_{i=1}^{S_{\max}} \sum_{j=1}^{S_{\max}} \frac{\partial p_i}{\partial N_j} \frac{d}{dt} \left[ \int_0^{A_j(N,t)} \left\{ \int_0^{G_j} n_{ju}(\mathbf{x}, \mathbf{n}, t) du \right\} d\mathbf{x} \right] \quad (6)$$

where  $i, j = 1, 2, \dots, S_{\max}$ . Note that population density at any one site must be summed across all ecotypes that exist at that location.  $G_j$  is the average number of ecotypes in the population, which is constantly changing over evolutionary time.

In addition to the two ecological processes responsible for the dynamics of population size of each species (i.e., local population dynamics and dispersal), a third process is added: genetic differentiation of ecotypes ( $dG_j/dt$ ). Dispersal in Eq. (6) not only has ecological consequences, but it is responsible for the genetic structure of the geographic population as well. The rate at which new ecotypes are produced is profoundly affected by this structure. All else being equal, the more *Wrightian* genetic structure a species exhibits, the lower the number of ecotypes that will be found within a population. The rate of extinction or extirpation of ecotypes increases with population subdivision because the rate of extinction of entire subpopulations is increased (due to low population

size). Furthermore, as genetic variation erodes in local subpopulations, the probability of generating new ecotypes by recombination decreases. Thus, the difference in the rate of per ecotype additions and deletions will be smaller, leading to fewer average numbers of ecotypes in the population. In populations with more *Fisherian* structures, loss of genetic variation by drift and extinction decreases and production of new ecotypes by recombination increases with increasing gene flow. The rate of origin of new species increases with increases in the rate of production of new ecotypes within species.

The structure of Eq. (6) implicitly includes the process of natural selection. This can be seen by considering the population dynamics of different ecotypes. Ecotypes that combine attributes in their phenotype that provide a better match for the resources found within the geographic range will produce more offspring. To the degree that these attributes are based on genotypes, offspring of the more successful ecotypes will inherit them, leading to proliferation of those genotypes and the reduction of genotypes that produce less ecologically successful ecotypes. Over time, natural selection may indirectly modify population structure by changes in relative frequencies of dispersal strategies. This would then change the genetic structure of the geographic range.

#### 4.2.4. Relationship between the microscopic and macroscopic descriptions

Eqs. (2) and (6) provide complementary descriptions for the evolution of average number of species within a group of related species. The meaning of the macroscopic parameters (additions and deletions of species in the fossil record) is seen by setting those to descriptions equal to one another, from which follows:

$$\lambda - \mu = S^{-1} \sum_{i=1}^{S_{\max}} \sum_{j=1}^{S_{\max}} \frac{\partial p_i}{\partial N_j} \times \frac{d}{dt} \left[ \int_0^{A_j(N,t)} \left\{ \int_0^{G_j} n_{ju}(\mathbf{x}, \mathbf{n}, t) du \right\} d\mathbf{x} \right] \quad (7)$$

Thus, rates of additions and deletions of species from a sequence of fossil forms over evolutionary time are averages across species of the consequences of genetic and ecological processes occurring within the geographical populations of the species involved.

From Eq. (7) we can draw some conclusions about the process of evolutionary diversification. Since the genetic structure of populations determines the rates of increase and decrease of ecotypes, it follows that genetic structures that increase rates of production of ecotypes or decrease their loss from the geographic population will increase the rate of diversification. Thus, clades that are collections of species with highly subdivided populations will tend to generate fewer species over time than those with lower subdivision. This conclusion follows from the ecological consequences of population subdivision. Smaller, more isolated subpopulations that represent distinct ecotypes will have shorter persistence times than larger, and less isolated subpopulations. Although population subdivision may enhance divergence among ecotypes, ultimately, it is the ability of ecotypes to persist over relatively long periods of ecological time that will influence the rates of speciation and extinction within the evolving clade.

What I have shown, then, in this section, is that the energy that enters into geographic populations of organisms, over long periods of time, maintains geographic populations within constraints imposed by the environments and genetic systems of species of species within evolving clades. The constraining influence of the genetic systems of each species, however, changes over time through the production of new ecotypes, each of which has a different set of optimal environmental conditions. Since environments change over evolutionary time, the composition of ecotypes within species changes. Eventually, no ecotype is found in a species that can survive under current environmental conditions, and the species as a whole goes extinct. Some species, however, produce an ecotype, or combination of ecotypes that are distinctive enough over evolutionary time to be recognized as new species, and thus, a new species is added to the clade. The spatial distribution of ecotypes across the range of a species plays a crucial role in determining the rate of production and loss of ecotypes in that species. Groups of related species within a clade will tend to have similar ecological attributes, and thus have similar types of spatial population structure and subdivision. Thus, the rate of change of species within a clade will be distinctive for that clade in the same way that the dynamics of population change will be distinctive for each species.

The statistical mechanics outlined in this section indicates that the general properties of the evolutionary process that has generated such a diversity of different kinds of plants and animals shares much in common with other complex systems. The details of what kinds of species are generated can vary substantially among different evolutionary lineages, yet a single macroscopic description suffices to describe the dynamics of diversification of all lineages. I emphasize that the statistical mechanics outlined above *does not* specify the particular outcome of the process for a specified group of related species. Rather, the model describes the general constraints within which the evolutionary process must occur. It can generate testable predictions. With a sufficiently detailed knowledge of the microscopic processes underlying the diversification of different clades, it is possible to predict a priori which clades will sustain the most species. For example, clades that contain widespread and abundant species tend to generate more species over evolutionary time than those with narrowly distributed species (Maurer, 1999).

Two important points should be noted about the model described in this section. First, the model does not require specification of the detailed molecular biology underlying the generation of new ecotypes. The mechanisms that underlie the generation of genetic diversity within a species form a complex system that is probably poorly known for many species. Certainly chromosomal structure and function will contribute to the generation of genetic diversity through processes like recombination, gene duplication, and movement of genes among chromosomes. The degree to which these processes are regulated is poorly understood (e.g., Lazyer, 1980; Dover, 1982). These genomic processes interact with ecological patterns of population subdivision to determine how the diversification of ecotypes within species proceeds for a given clade. Second, the model described above corresponds closely to the patterns of subdivision of seen within species. The growing science of phylogeography (Avice, 2000) is amassing a great deal of evidence regarding the geographic distribution of distinct lineages within species. These lineages correspond to the “ecotypes” described by the model. The more we understand about the phylogenetic structure of geographical populations, the greater our ability will become to begin to quantify

the microscopic processes underlying macroevolution.

## 5. Conclusions

The dynamics of geographical populations and the process of biological diversification can both be described in the same general way that one might describe any complex physical system. By focusing on energy flows that originate from organismal energy intake, and how these flows are constrained by environmental and genetic variation among individuals within species, it is possible to construct a statistical mechanics that describes macroscopic properties of these systems in terms of microscopic processes going on within them. In this respect, complex ecological systems can be thought of as exhibiting the same kinds of law-like behavior shown by other complex physical systems. Macroscopic order exists in ecological systems for the same reasons it does in geophysical, astronomical, and complex chemical systems. Order in any complex system can be studied by examining appropriate aggregates. For example, although no two stars are identical, the outline of their physical evolution emerges by examining the statistical properties of large numbers of stars.

Biologists and ecologists have tended to emphasize the uniqueness of living systems, arguing that they are qualitatively different from other kinds of complex systems. But, as Schrödinger (1944) pointed out, the differences are not as great as they seem. Physical order, as seen in the precise structure of crystals, for example, has a statistical basis. Most precise physical laws are precise at the macroscopic scale because they apply to large number systems that often are governed by strong constraints, not because they are not statistical. This understanding allowed Schrödinger (1944) to predict prior to the discovery of DNA that the underlying order of living systems must be attributable to an “aperiodic crystal”, which is an apt description of nucleic acids. What I have argued here is that ecological aggregates, observed at appropriate scales, exhibit statistical properties that describe an underlying order not evident at smaller scales (Brown and Maurer, 1989; Brown, 1995; Maurer, 1999). An understanding of this order produces macroecological laws that are empirically tractable and can produce

testable predictions. These laws should be considered models that produce descriptions of complex ecological systems, and not universal truths. The degree to which they are successful in producing a greater understanding about these systems will determine their ultimate usefulness.

The approach I have outlined in this chapter should be applicable to other complex systems, particularly those that are constrained by internal information, such as a genetic system. Within the framework outlined herein, information plays a relatively passive role by establishing constraints within which the dynamics of geographical populations occur. A complementary approach would be to describe population and genetic processes as information systems, asking how information accumulates and is dissipated over ecological and evolutionary time scales. The general informational dynamic would recognize that at any given point in time, a particular population (or clade) would be found in a small subset of states that it could possibly occupy. The “statistical entropy” of (or variability among) those states would be smaller than the maximum possible. The difference between maximum and realized statistical entropy can be used as a measure of ecological or evolutionary order (Frautschi, 1988; Layzer, 1988, 1990; Brooks and Wiley, 1988). In diversifying systems, such as a geographic population invading a new habitat, or a clade experiencing an evolutionary radiation, the order will increase as the realized statistical entropy (variability) of the system lags behind the maximum possible entropy. The extinction process would likely show a general decline in maximum statistical entropy<sup>1</sup> in concert with the realized statistical entropy of the system until the number of states available to the evolving system are so small that persistence is unlikely. If the realized entropy decays faster than the maximum entropy, then, paradoxically, order could continue to increase despite the increasing likelihood of extinction.

<sup>1</sup> A distinction must be made between the “statistical entropy” of the declining population that describes the number of possible states the population can occupy and the thermodynamic entropy of the universe that contains it. Maximum statistical entropy of the population can decline within the system because the matter and energy that determine the value of that entropy are dissipated as detritus and heat, increasing the thermodynamic entropy of the universe.

Ecological complexity is not devoid of order. With suitable definition of appropriate aggregates, such complexity can be treated as a statistical mechanical problem. The macroscopic laws thus obtained can be used to increase our understanding of the processes contributing to that complexity, and with sufficient data, might prove to usher in new theoretical treatments of ecological phenomena that in the past have proved difficult to study. The macroscopic laws described herein are in fact, ecological generalities, but not perhaps in the sense ecologists have looked for in the past. They have in their formulation specific requirements about the scale at which they provide useful scientific information. Inappropriate application of these laws to systems or experiments carried out at small scales will not provide useful tests of their predictions. Rigorous definitions of appropriate aggregates must precede any empirical treatment meant to provide strong tests of the predictions that might be derived from the models discussed herein. I anticipate that as such rigor is applied the models presented above, a greater understanding of ecological complexity will emerge regardless of whether these models are ultimately found to form a coherent theory or not.

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