

COMPLEXITY VERSUS DIVERSITY

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GLOSSARY

biotic interaction When the growth or behavior of one species affects those of another species; such interactions can be antagonistic (e.g., competition for limiting resources, predation, herbivory, or parasitism) or facilitatory (e.g., pollination or other forms of mutualism).

community Set of coexisting species in an ecosystem.

food web Set of trophic relationships among species in a community; schematically, the pattern often resembles a web of species each connected by trophic interactions with other species.

functional dependency Dependency of one species on another to complete a particular ecosystem process or function; an example would be the dependency of plants on decomposers and decomposers on plants to recycle nutrients.

phylogeny Pattern of evolutionary descent among species, generally illustrated as a "tree" in which nodes represent common ancestors and lengths of branches represent time since divergence; time since diver-

gence is generally assumed to correlate with genetic relatedness.

process intricacy Complexity of temporal or spatial patterns of ecological processes such as population dynamics or production.

structural intricacy Complexity of patterns of links or connections among species in a community that are created by biotic interactions, shared pathways of nutrient and energy flow, or phylogenetic relationships.

trophic interaction Feeding relationship between two species; these include predation, herbivory, parasitism, bacterivory, frugivory, or any other interaction that involves individuals of one species consuming individuals or parts of individuals from another species; trophic interactions represent a subset of all biotic interactions in a community.

ECOLOGICAL COMPLEXITY AND BIOLOGICAL DIVERSITY are often presumed to be strongly correlated or even synonymous with one another, but there is no necessary relationship between these terms. Ecological complexity is a scale by which we compare ecosystems. At one end of the scale, systems that exhibit unpredictable behavior or many connections among its species are considered "complex." At the other end of the scale, systems that exhibit highly predictable behavior or largely independent species are considered "simple." In

contrast, biological diversity is a measure of the extent of genetic and phenotypic variation found within a community. These two characteristics of ecosystems, complexity and diversity, though fundamentally related, are clearly distinct. Although diversity and complexity are not necessarily correlated, the potential for a community to exhibit complexity is likely to be associated with its diversity. Widespread changes in diversity experienced by most ecosystems have generated considerable interest in quantifying complexity and assessing whether current changes are affecting levels of ecological complexity in natural ecosystems. The resolution of issues surrounding the relationship between complexity and diversity is an active area in contemporary ecological research.

I. THE COMPLEXITY OF ECOLOGICALLY DIVERSE SYSTEMS

Hence, if certain insectivorous birds (whose numbers are probably regulated by hawks or beasts of prey) were to increase in Paraguay, the flies would decrease—then cattle and horses would become feral, and this would certainly greatly alter (as indeed I have observed in parts of South America) the vegetation: this again would largely affect the insects; and this, as we just have seen in Staffordshire, the insectivorous birds, and so onwards in ever increasing circles of complexity.

—CHARLES DARWIN, 1859

It is reasonable to believe that in following the numbers of orders in the fossil record we are indeed following the approximate overall course of ecological complication and diversification even though in a necessarily loose way.

—G. G. SIMPSON, 1969

Roughly speaking, we here take complexity to be measured by the number and nature of the individual links in the food web.

—R. M. MAY, 1974

The complexity of a system is in the eye of the beholder. It is measured by how well we understand causes, expect behaviours and, in praxis, achieve purposes. Hence, large numbers of variables, non-linear relationships among them, and the open nature of a system are important only to the degree they present barriers to understanding.

—C. S. HOLLING, 1985

A. The Complexity of Nature and the Entangled Bank

Darwin provided us with a wonderful metaphor for what is intuitively meant by “ecological complexity” in his famous closing passage to *The Origin of Specics*. In this passage, Darwin envisioned a riverbank teeming with a diverse and entangled array of organisms all involved in a complex web of biotic interactions. At the heart of this seemingly complex system, however, lies evolutionary and ecological processes that produce and maintain such remarkable diversity. For Darwin, biodiversity and the complexity that accompanies it are what distinguish nature from the inanimate features and processes of our world.

The entangled bank metaphor highlights two main ingredients of ecological complexity. First, there is biodiversity itself, with a clear implication that greater diversity provides a greater potential for complexity. Second, and more importantly, there is the web of interactions among species, with an equally clear implication that more complex webs (e.g., greater numbers and kinds of biotic interactions among species) are indicative of more diverse communities.

This metaphor also highlights two distinct meanings of complexity. First, complexity refers to the intricacy of the pattern of connections among species. This is the meaning used in many studies that have related ecological complexity to ecological stability. The second meaning applied to the term complexity is when nature defies easy characterization and cannot be reduced to a finite set of processes and principles that govern its order. This second meaning is used by the “macroecological” perspective (Brown, 1995), the hierarchical perspective of nature (O’Neill *et al.*, 1986), when considering nature as complex adaptive systems (Levin *et al.*, 1997), or when nature is viewed as a self-organizing system (Holling, 1992).

Figure 1 illustrates these different kinds of complexities. The top row of Fig. 1 shows the dynamics of an ecosystem process as an example of an ecosystem property that may exhibit simple or complex behavior. This process could be production, decomposition, or any other process representing the aggregate activities of species in the community. The remainder of Fig. 1 shows three fundamental kinds of linkages among species in communities: community structure or the biotic interactions among species, phylogenetic structure or the pattern of phylogenetic relationships among species, and functional structure or the pattern of functional dependencies among species. The pattern of tem-

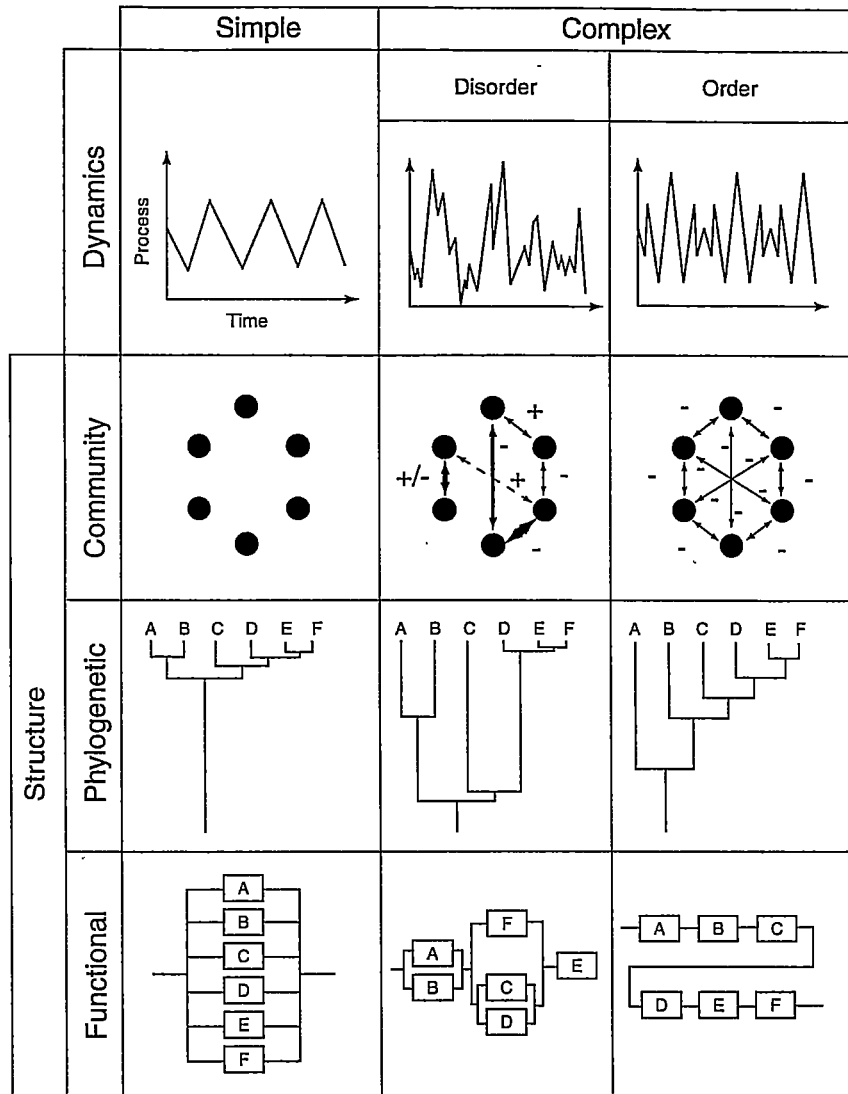


FIGURE 1 Simplicity and complexity in ecological systems. Dynamics are illustrated as temporal patterns in an ecological or evolutionary process, such as production, standing biomass, energy or nutrient flow, or rates of diversification. Community structure is illustrated as the number, type (e.g., competition or facilitation, shown as - or +, respectively), strengths (thickness of arrows), and arrangement of interactions (arrows) among species (circles). Phylogenetic structure is illustrated as phylogenetic trees in which every two species share a common ancestor. The vertical lengths of branches indicate distances, assumed to be a measure of genetic similarity or time since divergence. The complex phylogenies of more distantly related species contain more genetic information than would be found in the simple phylogeny of many closely related species. Functional complexity is illustrated as species whose contributions to ecosystem processes are either largely dependent (serially linked) on the activities of other species or exhibit a diverse array of interdependencies among one another. A simple system is one in which all species contribute to the functioning of an ecosystem in the same way (parallel redundancy) such that the loss of a species from a system does not affect its functioning.

poral or spatial variation of processes is known as process intricacy. The pattern of linkages, whether community, phylogenetic, or functional, is known as structural intricacy.

Whether considering process or structural intricacy, exhibiting either highly ordered states or highly irregular or disordered states is considered complex. As shown in Fig. 1, a temporal pattern for a specific ecological process that exhibits highly ordered, predictable, repeated series of oscillations would be considered complex. Yet a highly irregular, unpredictable, chaotic pattern of oscillation would also be considered complex when compared to a simple, mildly oscillating process. Similarly, Fig. 1 shows that a pattern of biotic interactions in which every species is linked to every species in the community by exactly the same kind of interaction with exactly the same strengths of interactions creates a symmetrical, highly ordered structure that would be considered complex. At the same time, a community that has a jumbled network of biotic interactions that vary in type and strength would also be considered complex when compared to a simple set of independent, noninteracting species.

Although ecological complexity is difficult to define precisely given the many different ways the term is used, when we consider the basic elements of ecological complexity it becomes apparent that diversity is not a necessary part of the definition of complexity. Note in Fig. 1, for example, that all nine structures shown are made up of six species. In spite of having the same number of species, these structures differ quite dramatically in complexity.

Despite the fact that diversity is not a necessary part of the definition of complexity, diversity and complexity are related in an elementary yet fundamental way. Few would debate that extremely depauperate ecosystems such as monoculture plantations of bananas are less complex than the extremely species-rich tropical rain forests they replaced, but for the bulk of ecological communities that lie somewhere between these extremes of biodiversity, determining just how complex a given system is can be quite difficult. For example, if a community contained 25 species of grasses while another contained only 10 species, but was made up of a mixture of 3 grasses, 4 forbs, and 3 shrubs, which community would be more complex? If a community consisted of 25 noninteracting species and another contained 5 species involved in a complex web of interactions, which would be more complex? If two communities each contained 10 species, but one exhibited chaotic dynamics while the other hovered close to a constant number of individuals per year in spite

of repeated perturbations, which would be more complex?

Another way to look at the problem is to plot, simply for illustrative purposes, complexity against biodiversity as done in Fig. 2. Aside from the trivial points where there is no diversity, and therefore no ecological complexity, and where there is some diversity and there is some complexity, a variety of relationships could be drawn between the two points depending on one's perspective or experience. That is, complexity and diversity could either increase hand-in-hand or show any possible relationship that is bounded by a positive, asymptotic relationship between diversity and complexity on one end and an exponential relationship between diversity and complexity on the other end (see Fig. 2). Of interest would be whether some general relationship could be described or whether every ecosystem would show a unique relationship. If the latter is true, then knowing a system's diversity would provide no means for predicting its complexity and whatever ecological behaviors might be a function of complexity.

Because ecological complexity is believed to be an important part of biologically diverse ecosystems and because diversity is currently rapidly declining, the role of ecological complexity is of considerable concern to ecologists. Does biodiversity loss mean loss of ecological complexity? If so, what are the ecological consequences of losing ecological complexity? This article reviews ecological complexity, its definition, its measurement, its relationship to biodiversity, and what is known about its role in ecosystem functioning.

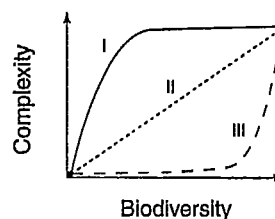


FIGURE 2 The potential relationships between complexity and biodiversity. Three possible relationships are shown. (I) The upper bound represented by an asymptote in complexity as biodiversity increases. (II) A linear relationship in which biodiversity is a direct measure of complexity in an ecosystem. (III) The lower bound represented by an exponential increase in complexity as diversity increases. Note that the general tendency is to quantify complexity as the number of interactions among species, and biodiversity as either species richness or the species richness weighted by relative abundance. Curve II represents the common perception of biodiversity and complexity being intimately related, but I and III represent the actual bounds for where the true relationship for a given ecosystem lies.

B. Concepts and Definitions

Concern over the potential alterations in ecological complexity caused by anthropogenic global change led the United Nations Environmental Program's Global Change and Terrestrial Ecosystem (GCTE) Core Project to establish Focus Four in 1996 to establish a research agenda for examining the ecosystem consequences of changes in ecological complexity. This program uses the following definition of ecological complexity:

Ecological complexity represents biological diversity but in a broad sense, including not only species diversity but also diversity of ecosystems and landscapes, as well as genetic diversity within species. In addition, ecological complexity involves the diversity of trophic pathways and interactions, that is, the connectivity of ecosystems. We can envision ecosystems with similar diversity but contrasting complexity as a result of different organizational structures.

—SALA, 1996

The first part of this definition of biodiversity was put forth in Article 2 of the 1992 Convention on Biological Diversity. In this Convention, biodiversity was defined as "the variability among living organisms from all sources including, *inter alia*, terrestrial, marine and other aquatic systems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems" (Harper and Hawksworth, 1995). This virtual synonymy with the first part of the GCTE definition of ecological complexity clearly indicates how strong a sense there is that biodiversity and ecological complexity are tightly correlated.

The second part of the GCTE definition concerns biotic interactions, which equates linkages among species with complexity. "Complexity," however, is not clearly defined, nor is it apparent from such a definition how one might go about measuring ecological complexity. Complexity is actually quite difficult to define and as a concept it has received far less attention than other subjects in the philosophy of science, but if we are concerned about its significance in ecological systems it would be valuable to begin by clearly delineating just what exactly is meant by "ecological complexity." In most instances, it is largely a matter of judgment that one thing is considered more complex than another, a judgment often based on a fair number of factors rather than just one or two. Thus it is not surprising, as dis-

cussed earlier, that species richness alone will fail to capture what is meant by ecological complexity.

Chapman (1985), in his review of a symposium on the concept of complexity, identified four distinct meanings of "complex" used in the conference and in the literature. First, there is what Chapman called "complication," or the process by which a system becomes naturally complex, but such complexity is ultimately "reducible" to fundamental principles or mechanisms. Second, there is "complication," which, like complication, concerns reducible systems, but involves purposeful design (e.g., a watch or a banana plantation has a different kind of complexity than the solar system or a tropical rain forest). Third, there is "complexification," which concerns irreducible systems (systems that are not composites of simpler parts). Finally, the fourth usage is "complexity" itself, which is simply a state of uncertainty concerning whether a system is reducible or not (irrespective of it being natural or of purposeful design). These decidedly ugly terms are not likely to catch on, but they do point to the variety of ways that ecologists, like other scientists, use complexity.

C. Community, Phylogenetic, and Functional Complexity

Typically, the web of interactions within a community, characterized by the number, nature, strengths, and structural pattern of biotic interactions among species, is often what is treated as ecological complexity. This can be the web of all interactions (community web, including competition, facilitation, parasitism, predation, and other interactions) or a subset of the community web, such as just trophic or feeding interactions (food web, including predation, herbivory, disease, or other consumer-resource species interactions).

In contrast to community complexity, however, phylogenetic complexity may be of interest when a community contains a diverse array of taxa. From the perspective of systematists or paleontologists, simply having many species that are phylogenetically diverse is evidence for complexity (Raven, 1996). A system of 15 species of grasses from the same genus might be considered less phylogenetically complex than a system of 10 species from 10 genera of grasses, which in turn might be less complex than a system with 5 species each from a different plant family.

Finally, complexity of an ecological system may be tied to its functioning as a biogeochemical system rather than to its population or biomass dynamics. That is, the flow of nutrients and energy through the system may be of interest rather than the dynamics of the

many populations found within it. Note that ecosystems function in the sense that they exhibit activity or processes such as nutrient and energy flow. "Function" need not imply purpose or design (an unfortunate connotation of the term "functioning").

From the foregoing, it is apparent that ecological complexity is a composite feature of ecosystems consisting of an extraordinary number of different factors, including population, phylogenetic, and functional characteristics of the species in the community. The full measure of the complexity of a single ecosystem would therefore include a large number of factors, most of which are difficult to quantify. In general, increases in any of the properties listed in Table I, whether associated with structural or process intricacy, tend to increase ecological complexity, whereas decreases tend

TABLE I
Measures of Ecological Complexity

Term	Measure	
Structural intricacy	Numbers of populations	
	Numbers of species	
	Numbers of biotic interactions	
	Kinds of interactions	
	Strengths of interaction	
	Higher-order effects	
	Indirect effects	
	Connectedness	
	Number of patches	
	Arrangement of patches	
	Immigration probabilities	
	Emigration probabilities	
	Number of functional groups	
	Number of functionally singular species (inverse of redundancy)	
	Number of links among functional groups	
	Number of compound functional groups (e.g., omnivores)	
	Phylogenetic distances among species	
	Phylogenetic moment	
	Process intricacy	Stability
		Predictability
Reliability		
Degree of nonlinearity		
Succession		
Population growth		
Ecosystem processes		
Extinction		
Speciation		

to simplify them. Table I demonstrates that measures of biotic diversity per se, such as species richness or evenness, are likely to be inadequate measures of complexity, though they may serve as crude proxy measures. The next section considers some basic measures of complexity, but not surprisingly, it will be evident that such measures of complexity generally deal with only single dimensions of complexity.

II. MEASURES AND CONSEQUENCES OF ECOLOGICAL COMPLEXITY

A. Measures of Complexity

Because complexity is a scale by which we compare communities and ecosystems, quantifying or measuring complexity is important in providing accurate means of making comparisons. Measuring complexity, however, is difficult because complexity is difficult to define. Boulding (1985) nicely described the problem at a United Nations conference held in Tokyo on the theory of complexity. He stated:

Complexity is a very complex concept, which is not altogether surprising. We do have a vague concept of it as a somewhat linear property, both of structures and processes, in which we make judgments of "more" or "less." I am pretty sure I am more complex than an amoeba.... Exact measurement of the concept eludes us and probably always will, for although we do make these estimations of it in terms of more or less, it represents a highly multidimensional reality that cannot be reduced to a linear measure.

In spite of the obvious difficulties Boulding outlined, ecologists and evolutionary biologists have nevertheless provided a number of measures of complexity, which are reviewed in the following sections. These measures can be used in conjunction with measures of diversity to assess the relationship between complexity and diversity.

B. Measures of Community Complexity

Measures of ecological complexity are closely allied with measures of diversity, which reinforces the common practice among ecologists of treating biodiversity and complexity as one and the same. At its simplest, one might consider diversity to simply be the number of species (S), or species richness. Such a measure is

often felt to be inadequate because it does not reflect differences in commonness and rarity nor the degree of connectedness among species. Thus, many other measures of diversity are used that attempt to take linkages or potential linkages into account. For example, the Shannon-Weaver index (H) considers both species richness and the relative abundances of species (evenness) as the important components of diversity. H quantifies diversity by assuming that richness and evenness directly represent the potential number of community configurations that a particular assemblage of species can produce. The original index quantified information, summing logged probabilities of a system having particular configurations.

The configuration of a community is seldom known, let alone the variety of possible configurations it can occupy or the probabilities of taking on these configurations. One therefore uses proportional abundances (p) of species as a means of approximating probabilities of configurations, a strategy that some consider fairly unsound.

The formula using this approach is

$$H = -\sum_{i=1}^s p_i \ln p_i \quad (1)$$

where i refers to the i th species in the community.

A related measure of potential complexity that compares the full potential with the realized potential for configurations is called connectivity (C), or the proportion of actual interactions (links or connections) to total possible interactions, which is distinct from food web connectance (see later). The formula for connectivity is

$$C = \frac{\sum_{i \neq j} a_{ij} p_i p_j}{\sum_{i \neq j} p_i p_j} \quad (2)$$

in which p is the probability of a species being present, and a_{ij} is the probability of interaction when two individuals, each from a different species (i and j), encounter one another. In reality, identifying interactions in biological communities is very difficult and cannot be deduced from abundance data. Indeed, Margalef and Gutiérrez (1983) explored connectance by examining components and "interactions" in functional plans for construction toys because information of equivalent clarity from real communities was unavailable.

The Shannon formalism serves as the basis for the preceding and other measures of complexity and diversity, but this practice is questionable. The Shannon

formalism quantifies complexity by estimating an upper bound for the number of configurations possible for a given set of entities as if all configurations would be functional. In reality, however, rules of assembly ultimately determine the actual limits of information that a set of entities can store and retrieve efficiently. For example, if one had a box of 26 unique letters (i.e., A–Z), each equally abundant, and a box of 4 unique nucleotides, each equally abundant, the Shannon formalism would consider the box of letters to have a greater capacity to store and retrieve information. Assembly rules for letters, however, must be followed to produce sentences containing useful information just as assembly rules for nucleotide sequences must be followed to produce useful proteins. It is quite possible that 4 nucleotides could code for a greater diversity of proteins in nature than 26 letters can code for words in English, the difference being attributable to the rules used in each system. Without knowing these rules, it is difficult to assess the actual information content for a collection of entities such as letters, nucleotides, or species. Although assembly rules for nucleotides and letters in human languages are well understood, assembly rules for species in communities, although well studied, are still poorly understood.

Appraisals of complexity based on static patterns of the distribution and abundance of species [Eqs. (1) and (2)] ignore flows of energy or nutrients and the dynamics of interacting populations, all of which are considered key elements of community complexity (see Fig. 1). Rutledge *et al.* (1976) adapted approaches based on information theory, as discussed earlier, to consider flows among species within a community. Their approach usefully distinguishes between and quantifies both flavors of complexity, that is, structured versus disordered patterns of flows among species.

Appraisals of community complexity may also be made using the pattern of biotic interactions that links species in a community. The notion that biotic interactions are the primary elements of structural intricacy (complexity) that determine community dynamics has been the dominant theme in community ecology for several decades, inspired by the original contributions of A. J. Lotka and V. Volterra. Mathematical treatments of complexity have explored the consequences of varying interactions by constructing model communities whose species richness, interaction coefficients, and signs and strengths of interaction vary randomly and by examining their stability features. The heart of this approach is to use the "community matrix" as a measure of complexity, a concept formalized by Richard Levins in 1968 and still very much in use today. The general

approach is to assume that all populations can be modeled by differential equations of the form

$$\frac{dx_i}{dt} = r_i x_i (K_i - x_i - \sum \alpha_{ij} x_j) / K_i$$

where r_i is the intrinsic rate of increase of the population of the i th species, K_i is the carrying capacity of the i th species, x_i is the population size of the i th species, and α_{ij} is the effect of the j th species on the i th species. For a community at equilibrium, where

$$K_i = x_i + \sum \alpha_{ij} x_j$$

the system of equations can be written as

$$AX \equiv K$$

Here, X is the column vector of species population sizes, K is the column vector of species-specific carrying capacities, and A is the community matrix

$$A = \begin{bmatrix} 1 & \alpha_{12} & \alpha_{13} & \cdot & \cdot \\ \alpha_{21} & 1 & \alpha_{23} & \cdot & \cdot \\ \alpha_{31} & \alpha_{32} & 1 & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & 1 \end{bmatrix} \quad (3)$$

The properties of this matrix can then be used in analyses of complexity. Although wonderfully appealing as a logical measure of community complexity, identifying and quantifying interactions in a community is a formidable task and requires that a community be at or near equilibrium, rarely the case in nature.

One concern over measures of structural complexity based on biotic interactions is that they must account for "keystone" species. Defined originally by R. T. Paine in 1966 as a predator species that fosters the coexistence of competing prey species and thereby promotes structural complexity in ecosystems, it has become colloquially used to describe any species that has a disproportionate impact on the community in comparison to other resident species (Liebold, 1996) or species that serve as ecological engineers (Jones *et al.*, 1994).

Power *et al.* (1996) proposed that the distribution of "community importance values" (CIVs) may serve as a tool for comparing communities for this element of structural complexity. Formally, the i th species in

a community has a community importance value (V) defined as

$$V_i = [(m_N - m_D)/m_N](1/p_i) \quad (4)$$

where $m_N \equiv$ the quantitative property (e.g., production or rate of decomposition) of the intact community, $m_D \equiv$ the quantitative property of the community with the i th species removed, and p_i represents the proportional abundance of the i th species before it was removed. In practice, one would sequentially delete one species at a time, each time measuring the community response to such a loss. Eventually a distribution of CIVs would be obtained and statistics (e.g., the mean or modal CIV and its variance) could be used to compare one community with another. Communities with mean CIVs furthest away from 0 would be more complex than those whose distributions were not significantly different from a normal distribution with a mean of 0. Of course, such an experiment would be very difficult to conduct and Power *et al.* (1996) could identify only two such studies.

One approach to the intractability of contending with all species interactions is to focus on a subset of interactions. An example of such a focus is the study of feeding or trophic interactions. Typically, food web statistics serve to quantify food web structural complexity. These statistics include food chain length, connectance (the ratio of existing trophic links to possible links), compartmentation (the number of compartments or isolated subnetworks of interacting species in a food web), the ratio of predator species to prey species, and interval versus noninterval state (presence or absence of complex overlaps in resource sharing). The difficulty with all of these statistics is that they rest entirely on the quality of the set of food webs, many of which were not constructed for such analyses, and thus produce artifacts when subjected to such analyses.

C. Measures of Functional Complexity

From a functional perspective, complexity may be measured as simply the number of functional groups. Functional groups may be considered collections of species that are related by their ecosystem activities, though many other definitions have been used. For example, if a functional group were defined as the group of species sequestering carbon from the atmosphere by photosynthesis, then all macrophytes, algae, and cyanobacteria found in a lake would be considered part of this

group, in spite of their very different ecologies and evolutionary histories. This degree of aggregation is much larger than what is typically found in contemporary food webs (trophic groups or species), community matrices (interaction coefficients from species pairs), or high-resolution phylogenies (orders, families, genera, species, etc.).

In the same way that tallying up numbers of species fails to capture complexity, tallying up functional groups is unlikely to serve as an adequate measure of functional complexity. More important would be the degree of parallel versus serial dependency among species in an ecosystem. As in community complexity, network architecture is the focus for measuring complexity, but rather than linkages of biotic interactions, only linkages of dependencies among species and functional groups become important.

Ecosystem reliability is an example of an index that combines measures of serial and parallel dependency (Naeem, 1998). Serial dependency occurs when every species or every functional group is dependent on the other for the ecosystem to function (e.g., decomposers depend on producers for energy while producers depend on decomposers for nutrient cycling). Parallel dependency occurs when one or more species within a functional group substitute for each other upon the extinction of one of the members of the group. In its simplest form, ecosystem reliability may be formally represented as

$$H(t) = \prod_{j=1}^F \left[1 - \prod_{i=1}^{S_j} (1 - e^{-\lambda t}) \right] \quad (5)$$

where F is the number of functional groups, S_j is the number of species in the j th functional group, and λ is the probability of extinction over a small increment in time, t . Note that the reliability of an ecosystem is defined as 1 [$H(0) \equiv 1$] and eventually decays in the absence of replacement of species by recolonization [$H(\infty) \equiv 0$].

As in other measures of complexity, the information needed for this index is difficult to obtain. Species, presence or absence, local extinction rates, and functional roles are often difficult to determine without considerable empirical work. Focusing on redundancy demonstrates, however, that if the properties being measured are the result of the collected activities of groups of similar (i.e., redundant) species, such as production, having many species could actually mean more steady levels of production (less complex behavior). Thus, the association between biodiversity and com-

plexity of ecosystem functioning is dependent on the degree of species redundancy in the system.

D. Measures of Phylogenetic Complexity

Whereas community and functional complexity focus on structural aspects of ecosystems, phylogenetic complexity examines the structure of the phylogenies that relate species to one another within a community by their evolutionary history. As with community and functional complexity, the number of species is an important starting point, but the architecture of the evolutionary "tree" or "bush," as opposed to network architecture, serves as the primary basis for assessing phylogenetic complexity.

A straightforward measure of phylogenetic complexity might be simply the sum of the lengths in the tree that unites all species in the set being examined or a simple modification of the Shannon-Weaver index in which species are weighted by their taxonomic distinctness. More informative, however, is the "phylogenetic moment" [defined in Eq. (6)], which provides a statistic by which communities might be compared. A difficult necessity for using this measure is that one has to have the complete phylogenetic tree at hand (referred to as tree T), including those species that might have gone extinct and might be missing from the local community being examined. The current community will consist of some subset of T (referred to as set R), and the local community that one is measuring will invariably be missing some species and contain an even smaller set of species (referred to as set r). If we assume that the tree (its nodes and branches) can be represented by a series of points in time, with a total of PT points for the whole tree, then the phylogenetic moment for this subtree (M_R) is

$$M_R = \sum_{p \in P_T} d_{pr_p} \quad (6)$$

where d_{pr_i} is the distance between a point on the tree and the nearest species in the set r . The smaller the phylogenetic moment is, the more closely the community represents the full phylogenetic structure (found in T). For example, in Fig. 3, although the total distances among the species in trees R_1 and R_2 are the same, using the phylogenetic tree T , which includes extinct species F and G and missing but extant species B , shows that R_1 would have a smaller phylogenetic moment than R_2 because C would have more near neighbors than D . That is, A , C , and E will presumably contain genetic

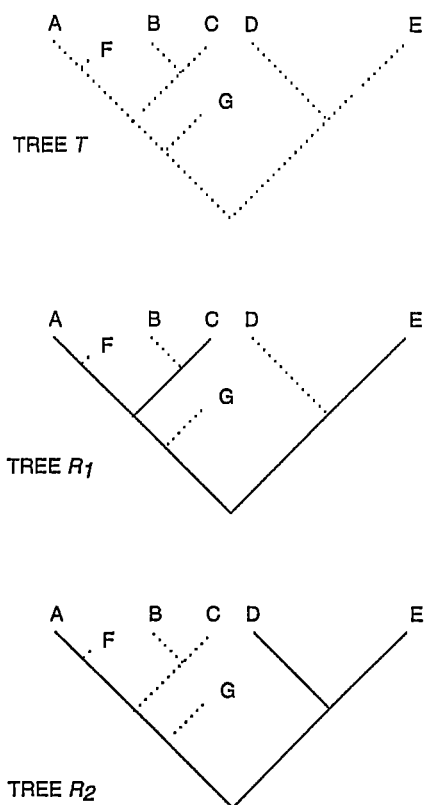


FIGURE 3 Hypothetical phylogenetic trees. Tree T represents the tree for all taxa in the community, including extinct species F and G. Two current local communities, each missing species B and one other extant species (dashed lines), are illustrated as R_1 and R_2 . Solid lines show trees that would be used in calculating the total phylogenetic distance among species. Note that they are the same for R_1 and R_2 . The phylogenetic moments for these trees would be the sum of the distances from each point on the tree T to the nearest species present. The moment would be smaller for R_1 .

information more representative of the bulk of the species in the full tree (T) than A, D, and E.

E. Utility of Measures of Ecological Complexity

Although several measures of complexity have been developed and explored [Eqs. (1)–(6)], in reality no single measure is likely to adequately describe ecological complexity in all its forms. Virtually any index based on a subset of the factors listed in Table I is likely to produce rankings in complexity that will not agree with other methods, much in the same way that different diversity indexes may disagree in how they rank communities. The quantification of complexity is hindered by the difficulty in uncovering all species and all their

interactions, their functional roles, and their phylogenetic relationships. As the next section shows, this means that we currently have only a partial picture of how complexity and biodiversity are related.

III. THE SIGNIFICANCE OF ECOLOGICAL COMPLEXITY

A. Complexity in Nature

Although diversity and complexity are practically universal features of ecosystems, we have much better information on diversity than on complexity. The estimation of existing diversity is, to be sure, challenging, but determining the distribution and abundance of species would only be the starting point for investigations of ecological complexity.

Unfortunately, the components of complexity are extraordinarily difficult to measure and for this reason empirical treatments have lagged behind the substantially greater progress made in theoretical explorations of the significance of ecological complexity. An ecologist never has a complete inventory of all species within a region, let alone their relative abundance, biotic interactions (direct, indirect, and higher order), phylogenetic relationships (at the regional level, including extinct species), functional roles, and population and process dynamics, or other details listed in Table I.

In most cases, however, the question at hand is more focused and thus more tractable. If the question concerns population stability, then quantifying only community complexity may suffice. If the question concerns what sets of species are most likely to contain the bulk of genetic information stored within a regional biota, then quantifying phylogenetic complexity may be enough. If the question concerns the magnitude or rate of ecosystem functioning, then quantifying functional complexity may do.

What is known about the relationship between diversity and complexity in nature? Several important patterns that emerge from studies that have examined community, functional, and phylogenetic complexity are considered here.

1. Community Complexity

An early and influential work that examined community complexity was R. H. MacArthur's 1955 study, inspired by E. Odum's theory that the "amount of choice which the energy has in following the paths up through the food web is a measure of the stability of the community." Using the Shannon-Weaver formula to model the num-

ber of alternative pathways and relate this to stability, MacArthur concluded that "stability increases as the number of links increases," though he was primarily considering resistance stability (remaining intact in spite of perturbation).

The theoretical relationship between complexity and stability is treated elsewhere in this volume, but it is worth noting here that this theory stimulated further investigations into the relationship between complexity and ecological processes, such as population dynamics. Later mathematical studies of local resilience stability (the ability to recover after perturbation) showed an inverse relationship between community complexity and resilience stability. Studies of connectivity and connectance (the nature and degree of connections among species) showed that resilience stability could either increase or decrease, depending on which trophic level was examined and the degree of connectance. Pimm (1979) also showed that complexity and stability could be positively related if one considered the deletion of species rather than resilience stability. Thus, those biologists who observed a positive association and those who observed a negative association between diversity and complexity more than likely differed in how they defined stability or how they defined complexity. Suffice it to say that there was agreement that complexity and stability were indeed related, but the nature of the relationship was dependent on one's definitions.

Although food web studies initially showed much promise as a means for examining the relationship between complexity (community structure) and diversity by focusing solely on trophic interactions, early findings did not fare well in the test of time. Polis and Winemiller (1996) summarize four patterns derived from early analyses of topographic or static food webs. First, there is constancy in the number of links per species in a food web irrespective of number of species. Second, the numbers of trophic levels seem to be invariably small (three or four). Third, the ratio of predator to prey species is relatively constant. Fourth, omnivory is rare. All of these patterns, however, have been challenged as artifacts.

Though potentially artifacts, food web patterns at least touched upon an obvious truth about communities—there are likely to be constraints in the structures of food webs. For example, at the simplest level, one cannot have consumers without resource species (i.e., no predators without prey) and there are likely to be stability or energy constraints that limit food chain lengths (Kaunzinger and Morin, 1998). Currently, food web biology has gone far beyond the sorts of patterns that initially stimulated research in this field, but new

patterns, if they exist, await the completion of a new set of higher-resolution food webs.

The main observation to be drawn from studies of community complexity is that complexity is never at its maximum in diverse ecosystems. For example, although the potential number of pairwise interactions is large for any community, few of these interactions may ever be realized. As Margalef (1985) states, "the considerations of artifacts [from mathematical studies of diversity and complexity] provide an elementary but effective approach to the assertion that no system is completely interlocked or connected." We may infer from this fact that complexity asymptotes with diversity, an important consideration in our quest to understand the relationship between diversity and complexity (see Fig. 2).

2. Ecosystem Functioning

Biodiversity and ecosystem functioning are treated elsewhere in this Encyclopedia, but here I examine its relationship to complexity and functioning. May (1974) noted in his "afterthoughts" to the second edition of his influential book that aggregate properties of communities, such as production (i.e., ecosystem functions), could show the opposite relationship with complexity that dynamic stability showed. Theoretical support comes from different approaches, but experimental tests of the idea are few. Support for this idea can be found in Tilman and Downing's (1994) study of experimental grassland plots, though some controversy surrounds this study. In their study, production recovery from a drought (resilience stability) increased with plant diversity. Two laboratory microcosm experiments using freshwater microbial communities by J. McGrady-Steed *et al.* and S. Naeem and Li (both conducted in 1997) showed that predictability and reliability of ecosystem functions, such as production and community respiration, can indeed be associated with biological diversity and complexity.

3. Phylogenetic Complexity

The relationship between phylogenetic complexity and biotic diversity is not well understood. Globally, estimates of origination and extinction of species suggest more or less steady increases in biotic diversity punctuated by aperiodic mass extinctions. This steady rise may be taken to mean that origination rates, over millions of years, have been outpacing extinction, except during periods of mass extinction, and that recovery from mass extinctions has always occurred. Such a history of the biota suggests to some that the biota can tolerate even very deep "prunings" of the tree of life. At a global level,

this suggests that random sets of species drawn from regional pools are likely to contain equivalent amounts of genetic information and that it takes severe levels of extinction to reach the point where insufficient genetic information is left in the remaining taxa to regenerate lost biodiversity. Because large-scale patterns in diversity across environmental gradients are similar across many taxa (Currie, 1991), we may expect that random samples from communities would result in phylogenies of similar complexity. Of course, since only a fraction of all species have been described, it is difficult to know exactly what the distribution and abundance of species are. As in community complexity and functional diversity, the true relationship between diversity and complexity is unknown, but it is likely to be asymptotic. That is, highly diverse systems may experience little change in phylogenetic complexity in the face of moderate levels of extinction.

V. CONCLUSIONS: THE DISENTANGLED BANK

Common usage of the term "complexity" in ecology implies that ecological complexity is a function of the phylogenetic, functional, and community structure of ecosystems. On the surface, ecological complexity and diversity seem so closely related that it is tempting to consider "biodiversity" as synonymous with "complexity." If we consider complexity to be the structural and process intricacies of a system, however, it is clear that diversity, in terms of numbers and types of organisms in a community, shows no necessary relationship with any measure of complexity aside from the trivial fact that without any diversity there is no complexity. Thus, two communities identical in numbers of species could be quite different in community, phylogenetic, or functional complexity. Likewise, a highly diverse system could be more or less complex than a depauperate system.

Studies of complexity in nature suggest asymptotic relationships between complexity and species richness, where species richness represents one way to define biotic diversity independent of complexity. It is hard to imagine, for example, that tropical rain forests, where species often number in the thousands, will show much reduction in complexity in the face of the loss of a few species. Current rates of extinction, however, are estimated to be staggeringly high and many diverse systems, such as tropical ecosystems, are not suffering extinction of species within their boundaries so much

as they are being transformed to depauperate, managed ecosystems.

Thresholds in the response of ecosystems to the loss of diversity are particularly of interest (Levin, 1997) and these may be hypothesized from current knowledge about the relationship between diversity and complexity. From what is known about nature, both theoretically and empirically, it is reasonable to postulate that both community and phylogenetic complexity show asymptotic relationships with diversity. Because functional complexity aggregates many species into small numbers of functional groups (e.g., all plants may be considered producers), we can postulate that the asymptote for functional complexity will be lower than that for community or phylogenetic complexity. When these are plotted together, as shown in Fig. 4, we can identify two thresholds of interest. At some point, admittedly difficult to define precisely without accurate measures of community complexity or phylogenetic complexity, one will continue to experience no appreciable loss in functional complexity, but ecosystem properties, such as dynamic stability, may change and genetic resources will decline. As diversity declines even further, functionality is eventually lost after the second threshold (the leftmost dotted line in Fig. 4) is crossed.

Managed ecosystems, such as aquaculture systems, farms, or monoculture tree plantations, most likely reside at the lower threshold, where the managers maintain the system at its minimal diversity. In general, these ecosystems may be functionally complete, containing all necessary functional groups to ensure that the desired ecosystem functions are maintained or, if not functionally complete, humans provide missing functions, such as fertilizer addition where nitrogen fixers have

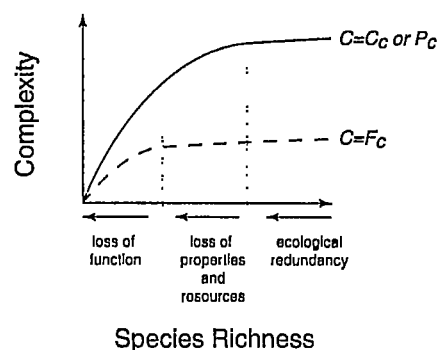


FIGURE 4 Hypothetical relationships between complexity and species richness. C = complexity. Vertical dotted lines indicate where the threshold in ecological consequences of declining ecological complexity might be identified. C_c = community complexity; F_c = functional complexity; P_c = phylogenetic complexity.

been removed. Complex systems are always more difficult to manage, but there are likely costs and consequences for resorting to simple systems, many of which have to do with system stability, system utility, and system efficiency, as the material in this article reveals.

The appropriate metaphor for the process of human transformations of ecological systems may be the disentangling of Darwin's entangled bank. As the earth's ecosystems are steadily transformed to agroecosystems and aquaculture systems, there is no question that average levels of biodiversity in ecosystems will continue to experience sharp declines in local biotic diversity, which eventually leads to losses in complexity. In many cases, understanding the ecological consequences of this loss may require focusing on ecological complexity, for which the quantification of species richness is only the first step.

See Also the Following Articles

DIVERSITY, COMMUNITY/REGIONAL LEVEL • FOOD WEBS • GENETIC DIVERSITY • LANDSCAPE DIVERSITY • MEASUREMENT AND ANALYSIS OF BIODIVERSITY • SPECIES DIVERSITY, OVERVIEW

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