

Disintegration of the Ecological Community

American Society of Naturalists Sewall Wright Award Winner Address*

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ABSTRACT: In this essay, I argue that the seemingly indestructible concept of the community as a local, interacting assemblage of species has hindered progress toward understanding species richness at local to regional scales. I suggest that the distributions of species within a region reveal more about the processes that generate diversity patterns than does the co-occurrence of species at any given point. The local community is an epiphenomenon that has relatively little explanatory power in ecology and evolutionary biology. Local coexistence cannot provide insight into the ecogeographic distributions of species within a region, from which local assemblages of species derive, nor can local communities be used to test hypotheses concerning the origin, maintenance, and regulation of species richness, either locally or regionally. Ecologists are moving toward a community concept based on interactions between populations over a continuum of spatial and temporal scales within entire regions, including the population and evolutionary processes that produce new species.

Keywords: biodiversity, biogeography, community ecology.

Recent symposia of the Ecological Society of America (Webb et al. 2006), the American Society of Naturalists (Harrison and Cornell 2007), and the British Ecological Society (Speciation and Ecology, Sheffield, March 29–30, 2007) have been devoted to phylogenetic and geographic approaches to the study of ecological systems, including ecological communities. This broadening perspective,

linked as it is to such disparate issues as global climate change and molecular phylogenetics, has stimulated ecologists to consider with more interest the history of the environment and the historical and geographic contexts of ecological systems (Latham and Ricklefs 1993a; Wiens and Donoghue 2004; Jaramillo et al. 2006; Ricklefs et al. 2006). We appear to be in the midst of a major synthesis in ecology (Lawton 1999), comparable to the maturation of ecosystem perspectives during the 1950s (McIntosh 1985) and population perspectives during the 1960s (MacArthur 1972; Kingsland 1985).

Despite these developments, however, ecologists, for the most part, continue to regard local communities as ecological units with individual integrity (Harrison and Cornell 2008). Empirical and experimental studies, including recent analyses of food webs and mutualistic networks (Jordano et al. 2003; Lewinsohn et al. 2006), circumscribe populations and communities locally (Morin 1999; Chase and Leibold 2003). Spatial scale rarely appeared in “community” theory until recently (Ives and May 1985; Brown et al. 2000; Leibold et al. 2004; McCann et al. 2005), and where it does appear, it is generally limited to the influence of dispersal limitation and population aggregation on local coexistence (Belyea and Lancaster 1999; Chesson 2000). The recent review by Agrawal et al. (2007) on “filling key gaps in population and community ecology” recognized some implications of the spatial and historical contexts of local “communities” (see Thompson et al. 2001) but emphasized the central role of species interactions on local scales in limiting coexistence. This is particularly significant because the Agrawal et al. review, with 16 prominent ecologists as authors, was commissioned by the National Science Foundation to recommend research priority areas in population and community ecology.

Evidence versus Belief in Community Ecology

In spite of decades of evidence to the contrary, ecologists have been reluctant to abandon a local concept of the

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community (Ricklefs 1987; Harrison and Cornell 2008). It has been eight decades since Gleason (1926) challenged Clements's (1916) perception of the community as an integral unit in ecology, and more than 50 years have passed since Whittaker's (1953, 1967) definitive work on the distributions of plant species across ecological gradients. In spite of the influence of MacArthur and Wilson's (1963, 1967) theory of island biogeography, in which colonization of islands from external sources was a primary driver of diversity, ecologists broadly began to accept the influence of regional processes on the species membership of local ecological assemblages only about 25 years ago (Hanski 1982; Cornell 1985; Ricklefs 1987; Pulliam 1988; Stevens 1989; Kareiva 1990; Cornell and Lawton 1992; Hanski and Gilpin 1997; Srivastava 1999). During this time, metapopulation ecology (Hanski and Gilpin 1997), landscape ecology (Turner et al. 2001), the mosaic theory of coevolution (Thompson 2005), neutral theory (Hubbell 2001; Hubbell and Lake 2003), macroecology (Brown 1995; Gaston and Blackburn 2000; Blackburn and Gaston 2001), and metacommunity perspectives (Holyoak et al. 2005), among other developments, have embraced large-scale patterns and processes.

New ideas and perspectives sometimes penetrate a discipline slowly, but ecology seems to have been especially resistant to the disintegration of the community as a central concept. (I use "disintegrate" in the sense of breaking an entity into parts or components or dispersing its cohesion or unity.) My own preoccupation with this idea might be misplaced, but Lawton (1999, p. 183) also emphasized, somewhat pessimistically, that "*the major weakness of traditional community ecology, and why it has so conspicuously failed to come up with many patterns, rules, and workable continent theory, is its overwhelming emphasis on localness.*" Perhaps strong local interactions are sufficient for an understanding of the structure of species assemblages, giving local communities, as well as the local populations they comprise, a primary ecological validity (MacArthur 1965, 1972; Cody 1974; Huston 1994; Belyea and Lancaster 1999; Weiher and Keddy 1999). Nonetheless, the persistence of the idea of local community integrity brings to mind two additional possibilities. One is a limitation of language. The words "population" and "community" have generally accepted definitions that correspond to entities, just like the words "dog" and "house," neither of which would withstand disintegration and still retain its essential features. The second is a problem of utility. Disintegrating "community" might be justified, but would this inform our science? That is, would significant and compelling new theory and research programs materialize? I argue here that local coexistence can be understood only in terms of the distributions of species within entire regions, which are determined by diversifi-

cation and adaptation within the regional ecological space in combination with the interactions of species over entire regions (Ricklefs 2007b).

Local Communities Are Not Integral Entities

Ecologists consistently define communities as units: generally, populations of different species living within a specified location in space and time. Although this definition need not connote an integral nature, common usage in ecology implies (artificially) bounded units that may be treated as entities. These units are also fixed in a hierarchy of organism-population-community-ecosystem-biosphere (Lidicker 2008) and are generally taught in this order in introductory ecology courses (e.g., Molles 2005; Smith and Smith 2006; Cain et al. 2008). The idea that a local assemblage consists of species with partially overlapping distributions that happen to co-occur at a point—Gleason's (1926) individualistic concept of the community—does not easily fit into this hierarchical concept, for example, in the way that species fit into genera and genera make up families. Ecologists generally accept that populations have a spatial extent and are integrated by the movement of individuals within them (Pulliam 1988, 2000; Loreau and Mouquet 1999; Amarasekare and Possingham 2001). From this perspective, a local community cannot be inclusive of the populations of its component species.

Of course, populations have geographic structure defined by barriers to dispersal, which result in interrupted gene flow, isolation by distance, and local genetic and ecotypic differentiation. Sewell Wright (1978) made seminal contributions to understanding spatial population structure. Dispersal limitation has infused work on species interactions as well, for example, through Thompson's geographic mosaic of coevolution (Fox and Morrow 1981; Thompson 2005; Siepielski and Benkman 2007) and Hubbell's metacommunity construct (Hubbell 2001; Condit et al. 2002; Chave 2004; Holyoak et al. 2005), which partitions ecological systems into local and global entities connected by a migration parameter (m). Dispersal limitation is necessary for allopatric speciation (Coyne and Orr 2004; Price 2008), a process that is often linked to global variation in species richness (Mittelbach et al. 2007). Dispersal limitation within metacommunities produces a theory of species-area relationships and beta diversity (Hubbell 2001; Condit et al. 2002). Regardless of the degree to which populations are subdivided, however, they exhibit integration over spatial scales that greatly exceed the generally accepted extent of local communities.

Disintegration of local communities, made necessary by the spatial extent of their component populations, frees one to address the geographic distributions of populations and the historical development of local assemblages of

species (Ricklefs 1989; Webb et al. 2002; Cavender-Bares et al. 2006). One can then ask whether assemblages achieve local equilibria or, conversely, whether local diversity reflects regional rates of species production and extinction (Cardillo 1999; Cardillo et al. 2005; Allen et al. 2006; Ricklefs 2006b), constraints on adaptation within ecological space (Wiens and Donoghue 2004; Ricklefs 2006a), and dispersal limitation through geographic space (Svenning and Skov 2004; Vormisto et al. 2004). Regional perspectives reveal departures from local equilibria, discussed below, that bring into question the development and testing of theory based on local coexistence.

Disintegration raises the issue of scale in ecology (Allen and Starr 1982). When boundaries break down and pattern and process lack discrete spatial extent, time and space become continuous (Shurin and Srivastava 2005). Within large regions—continents or major ocean basins—processes with different extents in time and space influence the diversity of species over a range of scales. At the “regional” end of the spectrum, matching the distributions of entire species, allopatric speciation is the creative engine of species richness (Cardillo et al. 2005; Jablonski et al. 2006; Ricklefs 2006b; Roy and Goldberg 2007; Weir and Schlüter 2007); shifts in topography and climate, as well as catastrophic events with regional effects, can also reduce species richness at these large spatial scales. At the “local” end of the spectrum, matching the dispersal distances of individuals within populations, competitive and other interactions between species assume greater importance (MacArthur 1970; Brown 1981; Brown et al. 2000). Intervals between speciation and catastrophic events, as well as the intervals required for substantial climatic and topographic change, are much longer than the intervals between births and deaths that determine local changes in population size (Schneider 1994, 2001).

History, Geography, and the Community Concept

MacArthur (1965) argued that one could ignore large-scale history and geography in the study of ecological communities because local processes influencing the coexistence of species (i.e., competition, predation, and mutualism) come into equilibrium locally so rapidly that processes on larger scales are inconsequential. Thus, local assemblages have limited membership determined by species interactions (MacArthur and Levins 1967; Vandermeer 1972). Accordingly, variation in diversity should reflect the way in which physical conditions influence the coexistence of species, leading to the prediction that species richness should vary in direct relationship to the environment, particularly climate (Ricklefs 1977; Currie 1991; O’Brien 1998; Hawkins et al. 2003; Currie et al. 2004; Kilpatrick et al. 2006). A second important prediction from this idea is

that local species richness should be independent of regional species richness (Terborgh and Faaborg 1980), in which case discrepancies between the two would be explained by differences in species turnover among habitats or over distance: beta diversity (Cody 1975).

The recent literature in ecology has addressed these predictions in detail, producing two general conclusions. First, species richness is generally related to physical conditions of the environment—temperature and water availability, for example (Hawkins et al. 2003)—although diversity on both regional and local scales can differ between regions with similar environments (Ricklefs and Latham 1993; Hugueny et al. 1997; Qian and Ricklefs 2000; Ricklefs et al. 2006). The diversity-environment correlation need not imply local equilibrium with respect to physical conditions. A close relationship between the two is also predicted by hypotheses based on evolutionary diversification out of ecological zones of origin (Terborgh 1973; Latham and Ricklefs 1993b; Wiens and Donoghue 2004; Ricklefs 2006a). Second, where tests are feasible, generally in intercontinental comparisons, local species richness is directly related to regional species richness (Fjeldså and Lovett 1997; Srivastava 1999; Ricklefs 2000; Rahbek and Graves 2001; Shurin and Srivastava 2005; Rahbek et al. 2007; see Hillebrand and Blenckner 2002 concerning the value of these tests). This suggests that large-scale processes (species production and regional extinction) influence both regional and local diversity or, alternatively, that environmental conditions similarly influence processes on both regional and local scales. These alternatives can be tested statistically with structural equation modeling (e.g., Harrison et al. 2006). Differences in diversity in similar environments in different regions—so-called diversity anomalies—imply that large-scale regional and historical factors can influence local species richness over and above the influence of the local environment (Latham and Ricklefs 1993a; Ricklefs and Latham 1993; Qian and Ricklefs 2000; Ricklefs et al. 2006).

According to the theory of ecological drift (Hubbell 2001), the equilibrium number of species within a meta-community is a function of the speciation rate and the total number of individuals, which generally varies with the size of the region. If speciation rate were influenced by environmental conditions (Davies et al. 2004; Allen et al. 2006), this theory also would produce diversity-environment relationships, as well as a correlation between diversity and the size of a region (Terborgh 1973; Rosenzweig 1995; Ricklefs 2006b). Hubbell’s model also predicts a direct relationship between the number of species in a local assemblage and regional diversity, determined by the balance between species production and dispersal. Ecological drift ignores obvious ecological factors—particularly environmental variation and habitat specialization—

but nonetheless emphasizes the connection of local diversity to large-scale processes. Alas, community drift is much too slow to account for observed rates of species turnover (Leigh 1981, 2007; Nee 2005; Ricklefs 2006c), just as genetic drift is slow compared to adaptive evolution. Consequently, only more powerful evolutionary and ecological forces can account for patterns of species richness.

The Regional Community Concept

How can we reconcile these observations: diversity-environment relationships, local-regional diversity relationships, and regional effects (diversity anomalies)? By replacing artificial local-community boundaries with a time-space continuum of process and pattern in population and community ecology (Shurin and Srivastava 2005), we might imagine processes of large and small extent tending toward equilibrium over a continuum of scale. Accordingly, distinguishing within-habitat and between-habitat components of diversity would become arbitrary and lose meaning. This applies to Whittaker's (1960, 1972) alpha diversity, which addresses the number of species within a particular area, community, or ecosystem. Alpha diversity may be defined for an area as small as a local plot or as large as an entire region, at which point it is identical to regional, or gamma, diversity. Beta diversity, which describes the rate of change, or turnover, in species composition across habitats or among communities, thus loses meaning because it depends on the scale of the alpha component of diversity, emphasizing the continuity of pattern over space (Loreau 2000) or time.

The “open-community” perspective of Gleason (1926), supported by Whittaker's depictions of the distribution of populations over ecological gradients within regions (Whittaker 1967), signaled a major shift of emphasis that has yet to materialize fully, in spite of the widespread application of ordination and other approaches to handling spatial variation in ecology (Legendre and Legendre 1998). The local community concept represents what I think of as a vertical perspective on species occurring within an arbitrarily bounded area, vertical because the species present locally add together—pile up, so to speak—to form the local assemblage. The occurrence of species elsewhere within a region is of no consequence. In contrast, the regional community concept corresponds to a horizontal perspective on the distribution of populations over ecological and geographic gradients (e.g., Pulliam 2000; Pyke et al. 2001; Phillips et al. 2003; Wiens et al. 2007; Butt et al. 2008). Each distribution reflects the ecological heterogeneity of a region, the adaptations of individuals to physical conditions, vegetation structure, and so on (i.e., the fundamental niche), the ability of individuals to disperse to isolated suitable areas, and the pro-

ductivity of a population as it is influenced by its evolved interactions with resources, competitors, and consumers (i.e., the realized niche).

Developing a Regional Perspective

From the distributions of species along environmental or geographic gradients, the local community can be reduced to a single point shared by many species. Lacking spatial extent, this “point community” ceases to be an entity. The community concept is replaced by the spatial distributions of populations, which now become the primary focus for understanding biodiversity patterns. Accordingly, the beta (spatial) component of diversity is defined by the extent of each population over space or over an ecological gradient, shifting our focus from the local community to the individual population within the region.

Imagine an ecological gradient of length V harboring species (populations) that occupy average length v . The probability that a particular species occurs at a particular point is v/V , and the average point diversity is thus $S \times (v/V)$, where S is the number of species in the region. Point diversity varies in direct relation to both S , reflecting large-scale processes that determine regional species richness, and v , the outcome of processes that determine the ability of a population to spread and maintain itself over an ecological or spatial gradient. These processes include species interactions over the entire region. One outcome of these interactions is that each population will approach a stable “carrying capacity” over the region as a whole, being confined by consumers and competitors to favorable parts of the ecological space in which births plus immigration balance deaths plus emigration, on average. The resulting demographic equivalence of all species within a region allows slow processes, such as the production of species, to influence S ; to the extent that higher S results through regional competition in smaller v , regional processes influence point diversity as well (Ricklefs 1989).

To adopt a regional, or horizontal, perspective, ecologists must turn their attention away from local assemblages and toward populations, which, while not completely discrete entities, interact with other populations over their entire distributions. Ecologists have yet to develop a theory tying together the ecogeographical distribution and local abundance of populations, although this is a key issue in the agenda of macroecology (Brown 1995; Gaston and Blackburn 2000; Gaston 2003) and, to some extent, meta-community ecology (Holyoak et al. 2005). At the core of this issue is the concept of the niche, referring to the occupation of ecological space (Brown 1981, 1984; Pulliam 2000; Chase and Leibold 2003). In locally defined community ecology (the vertical perspective), the niche reflects evolved attributes of individuals for exploiting resources.

The horizontal perspective implies an additional, between-habitat, or population, component to the niche, shaped by the spatial dynamics of populations that link interactions among species over large regions.

Filling Regional Ecological Space

Can the regional-horizontal perspective produce new insights and promote the development of new theory in ecology? A pessimistic answer would be that spatial components of population processes and consideration of both individual and population components of niche space create unmanageable complexity (Lawton 1999; McPeek and Brown 2007). The dynamics of species production and evolutionary adaptation, as well as the causes and uncertainties of extinction, pose additional challenges. Diversity unfolds within a region as evolving clades of species grow and shrink. Evolutionary conservatism of ecological relationships (Westoby et al. 1995; Ackerly 2003, 2004; Westoby 2006) constrains the way that species fill regional niche space (Webb et al. 2002; Cavender-Bares et al. 2004; Silvertown et al. 2006a, 2006b).

An important issue is whether, barring environmental catastrophe, the number of species within a region typically achieves equilibrium, with balanced rates of speciation and extinction. Is diversity stably regulated within regions? Analyses of changes in diversification rates based on phylogenetic data (Pybus and Harvey 2000; Nee 2006; Rabosky et al. 2007) suggest that many clades show early bursts of diversification followed by relative quiescence (e.g., Lovette and Bermingham 1999; Harmon et al. 2003; Kozak et al. 2006).

Analyses of diversity in the fossil records of several groups have revealed relative constancy in the number of species over periods of tens of millions of years (e.g., Alroy 2000; Jaramillo et al. 2006; Alroy et al. 2008). The independence of clade size and age reported in flowering plants (Ricklefs and Renner 1994; Magallón and Sanderson 2001), birds (Ricklefs 2006b), and squamate reptiles (Ricklefs et al. 2007; cf. McPeek and Brown 2007) further indicates that the regional diversity within individual clades, and perhaps within entire biotas, is regulated, at least relative to the turnover of species within clades (Ricklefs 2007a, 2009; Rabosky and Lovette 2008). Changing environmental conditions or the appearance of key evolutionary innovations might result in the ascendancy of a particular clade at the expense of others (Rabosky et al. 2007). Such trends are slow compared to intervals between lineage splitting and extinction but much more rapid than predicted from the dynamics of random events (Ricklefs 2007b).

The Regulation of Species Richness

The regional perspective challenges us to understand the factors that determine the number of species within a region and how this number is linked to the geographic and ecological distributions of individual species. The absence of a diversity-age relationship among clades suggests that regions have carrying capacities for species as well as for individuals. Carrying capacities for populations can be linked to the relationship between resource availability and individual resource requirement. A carrying capacity for number of species is more problematic. Ricklefs (2009) found that the numbers of species in orders of flowering plants and tribe- to family-level clades of passerine birds were correlated between continents. This result suggests that, to the extent that diversification of these clades has been independent in the different regions, each clade achieves a similar equilibrium number of species. Accordingly, not only would the total number of species within a region be regulated but individual clades also would appear to be constrained within the total regional ecological space.

The size of a clade tends to vary in proportion to the size of the region in which it has diversified (Ricklefs 2006b; Ricklefs et al. 2007). If clade size were a regional property, it could be determined by increased rates of species production (and less frequent extinction) in a larger regional area or by the ability of large regions to accommodate more species when physiographic and ecological complexity provides opportunities for allopatry and population turnover. Equilibrium island biogeography theory (MacArthur and Wilson 1967) states that diversity responds to the pressure of colonization and also reflects island-size-dependent extinction (e.g., Ricklefs and Bermingham 2002, 2004). When islands are large enough, internal species production further elevates diversity independently of an island's range of environments (Losos and Schlüter 2000). Thus, in island systems, both local and regional (=island) diversity reflect forces that are external to the ecological characteristics of local habitats or the habitat heterogeneity of an island. We need to extend our spatial scale only slightly to suppose that continental biotas come under the influence of similar considerations.

Ecologists understand in detail the foundation mechanisms of evolutionary adaptation, physiological limits to distribution and production, population dynamics and species interactions, and the trophic structure of ecosystems. However, the expression of these mechanisms in a complex world with a long history is bound to be idiosyncratic and unpredictable, just as evolutionists, with their detailed understanding of the mechanisms of heredity and selection, might fail to predict the existence of kangaroos, for example. Nonetheless, nature, including its di-

versity, does exhibit pattern, and it should be possible to understand the origin of that pattern.

The Future of the Community Concept

I return to the question posed earlier in this essay, namely, can the disintegration of the concept of “community” lead to new theory and research? My answer echoes E. O. Wilson’s (1959, p. 122) admonition a half-century ago that there is “a need for a ‘biogeography of the species,’ oriented with respect to the broad background of biogeographic theory but drawn at the species level and correlated with studies on ecology, speciation, and genetics.” The local “community” consists of those species whose distributions include a particular point in space and time. However, the integral units of community organization are the populations of species within regions that might or might not encompass that point. Indeed, the presence and relative abundance of a species at a particular point might depend on interactions with populations that do not occur there. Thus, to understand the coexistence of species locally, one must understand what shapes species distributions within regions. The statistical nature of these distributions has been a concern of macroecology (Brown 1995; Gaston and Blackburn 2000; Gaston 2003), but factors that constrain distributions within regions are poorly understood. Ordinations of species across sample locations often have high dimensionality, indicating multiple influences and possibly idiosyncrasy and randomness in distributions; correlations of ordinated positions of species with environmental variables tend to account for little of the total variance in the species distributions (e.g., Eilu et al. 2004; Svenning et al. 2004).

The characteristic dimension (v_i) of the distribution of species i within a region is influenced by the range of ecological conditions to which individuals are adapted (Brown 1984; Gaston 2003); genetic differentiation of local populations within the species’ range (Thompson 2005); accessibility of ecologically suitable areas relative to dispersal capabilities of a species (Pulliam 2000; Svenning and Skov 2004); historical changes in the distribution of ecological zones within a region (Brown et al. 2000; Linder 2005; Galley and Linder 2006); ancestral connections with related species within a region (Barracough and Vogler 2000; Wiens and Graham 2005; Lovette and Hochachka 2006; Wiens et al. 2007); and interactions with competitors, predators, and pathogens, as well as species in mutually beneficial associations (Belyea and Lancaster 1999; Kelt and Brown 1999; Weiher and Keddy 1999; Brown et al. 2000). Patterns of diversity within regions integrate mechanisms that produce new species, cause extinction, and effect the ecological and geographic sorting of species.

At the beginning of this essay, I asserted that the dis-

tribution of species within a region is more fundamental biologically than the coexistence of many species at a point. This assertion implies that, in focusing on local diversity, we have been asking the wrong questions or, perhaps, the right questions on the wrong scale. New understanding in community ecology will come from investigating factors that influence the distributions of species across space and across gradients of ecological conditions. The task is made difficult by the fact that each species may evolve a unique relationship to the environment, leading to idiosyncratic distributions that bear no general relationship to environmental conditions. Moreover, species interact within the regional as well as the local context, and the packing of species into ecogeographic space bears an unknown relationship to their packing into local ecological niche space. Indeed, the partitioning of local space might be considered a by-product of these larger-scale processes.

Species distributions reflect the interaction of the adaptations of individual species in the ecogeographic setting of a region, including historical changes in the distribution of environments and dispersal barriers and corridors. The region itself can be described in terms of the range and geographic distribution of its environments. The relationships of species to the environment can be as varied as the ways in which species can become specialized. Nonetheless, phylogenetic conservatism of habitat requirements and distribution patterns can organize the bewildering variety of patterns and provide clues to dominant influences of species characteristics on distributions. The influence of species interactions, especially competition, on distributions might be sorted out, in part, through the relationship of distributional overlap to niche separation. Most of these approaches are incorporated into the varied research programs of contemporary ecology but have yet to be integrated into a restructuring of community ecology.

What about the use of the word “community”? It should be kept, because populations do interact within entire regions, but it should be associated with an expanded concept of the historical and spatial dimensions of these interactions. We should acknowledge that populations are the primary entities in community ecology and that the region is the appropriate scale for an ecological and evolutionary concept of community.

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