

## EVOLUTIONARY DIVERSIFICATION AND THE ORIGIN OF THE DIVERSITY–ENVIRONMENT RELATIONSHIP

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**Abstract.** Global patterns in species richness have resisted explanation since they first caught the attention of ecologists in the 1960s. The failure of ecology to fully integrate the diversity issue into its core of accepted wisdom derives from an inappropriate concept of community and the rejection of history and region as formative contexts for ecological systems. Traditionally, ecologists have held that the pervasive relationship between species richness and conditions of the physical environment reflects the influence of environment on the ability of populations to coexist locally. However, many ecologists now recognize that this relationship can also develop historically from the evolutionary diversification of lineages within and between ecological zones. To assess the relative roles of local ecological constraint vs. regional and historical unfolding of diversity–environment relationships, we must abandon localized concepts of the community and adopt historical (particularly phylogenetic) and geographic methods to evaluate the evolution of diversity within large regions and its influence on diversity at local scales. This integrated perspective opens new research directions for ecologists to explore the formation of species, adaptive diversification, and the adjustment of ecological distributions of species on regional scales.

**Key words:** adaptation; community; diversity gradient; history; local determinism; phylogeny; saturation; speciation; species packing; species richness.

### INTRODUCTION

The number of species at all spatial scales varies widely over the surface of the earth. Ecologists have sought explanations for patterns of diversity in the varied expression of ecological processes under different local physical conditions of the environment. However, patterns in diversity also can be explained plausibly as the outcome of large-scale processes that control the production and extinction of species within regions, which in turn influence the number of species in local assemblages. These alternatives are not mutually exclusive, and ecologists are beginning to join features of both into a unified theory for the origin and maintenance of patterns of diversity. The task is more difficult than it would seem, because it requires the integration of dissimilar properties of biological systems: deterministic properties that are molded by local ecological processes, and the outcomes of evolutionary and biogeographic processes that depend on unique features of the history and physiography of regions (Ricklefs 2004, 2005a). Because local determinism has been so prominent in ecological thinking, I first consider how local determinism has achieved its current status, then briefly review some of the conflicting data that weaken this central ecological paradigm, suggest ways in

which the relative contributions of local and regional processes can be weighed, and sketch out some implications of diversity patterns for our concepts of ecological systems.

All biological systems have *general properties*, which are governed by the pervasive influences of thermodynamics, evolutionary adaptation, and other ubiquitous processes. They also have *special properties*, which reflect the unique history and present-day circumstances of every species and location. These special properties form the foundation of systematics and biogeography. Ecologists traditionally have been concerned with general properties of systems arising from universal processes with deterministic outcomes. Ideas about the distributions of organisms, population regulation, population interactions, community succession, and ecosystem energetics have stemmed from such thinking (Kingsland 1985, McIntosh 1985, Brown et al. 2004). Global patterns of species richness occupy an uncertain position between the special and the general. Early treatments regarded such patterns as the special outcome of history and, therefore, outside the realm of ecology (Wallace 1878, Matthew 1915, Willis 1922, Fischer 1960). Tropical diversity was thought to reflect the greater age, area, and climatic stability of equatorial, compared to temperate and boreal, environments, which allowed ample time and opportunity for the evolution of diverse forms of life (Dobzhansky 1950, Pianka 1966).

### THE RISE OF LOCAL DETERMINISM

With the development of community ecology as a mature discipline in the 1960s, ecologists began to regard

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diversity as a general feature of biological systems regulated locally by processes with deterministic outcomes (MacArthur 1965, 1972). Moreover, because local population interactions achieve equilibrium within tens of generations, they were thought to be fast enough to override more ponderous regional and evolutionary processes (Ricklefs 1989). These considerations led to a theoretical construct wherein population interactions limited membership in a community to species that are ecologically compatible (MacArthur 1968, May 1975, Case 1990, Morton et al. 1996). Accordingly, differences in the number of species between communities reflected the different outcomes of species interactions under particular environmental conditions. This implied that diversity would be correlated with variation in the physical environment, which has been borne out, to greater or lesser degree, by empirical studies (e.g., Mittelbach et al. 2001, Hawkins et al. 2003b).

Ironically, the rise of *local determinism* in community ecology occurred almost simultaneously with two other developments that contradicted its basic tenets. The first was the acceptance by most ecologists of an “open” community structure (Gleason 1926), which is to say that communities lack boundaries and that locally coexisting species have more or less independent distributions over spatial and ecological gradients within regions (Whittaker 1967). The second was the colonization–extinction steady state in MacArthur and Wilson’s equilibrium theory of island biogeography (MacArthur and Wilson 1967), in which local (island) diversity is responsive to an external driver (colonization).

Referring to the number of species on islands of different size close to the source of colonization, MacArthur and Wilson (1963) introduced the idea of *saturation*. In their meaning of the word, saturation was not a local property, but reflected the influence of the size of an area on sampling properties and rates of extinction of populations. Abbott and Grant (1976) also used this concept of saturation to represent diversity within a particular continental source area for colonists, against which the diversity of islands could be measured. These empirical concepts were transferred to local communities through theoretical analyses of limiting similarity among species (e.g., MacArthur and Levins 1967), which led to the idea of *species packing* and its corollary that diversity (species coexistence) was constrained by the capacity of the local environment to support interacting species. During the following decade, ecologists conducted comparative studies of communities largely in the context of species packing and the partitioning of niche space, presuming that environment constrained diversity (e.g., Pianka 1973, Cody 1974).

In fact, community theory sets no upper “saturated” limit to diversity in a particular environment. Referring to a community of competing species, MacArthur (1970) emphasized that “... in a constant environment there is almost no limit to the number of species which can improve the fit and hence be packed in ...” However,

the flexible filling of niche space was too complicated to be handled by theory. Eventually, local community ecology was insulated from such external drivers as colonization and regional species production. Many ecologists accepted local saturation, and they reconciled differences between local and regional diversity by differential turnover of species between habitats (beta diversity; Cody 1975). Thus, while recognizing the influence of large-scale processes on regional diversity, most ecologists still regarded patterns of local diversity as the consequence of ecological sorting of species available within a region (MacArthur 1965, Diamond 1975, Zobel 1997, Weiher and Keddy 1999).

#### NEW CONCEPTS OF ECOLOGICAL COMMUNITIES

Recent excitement over Hubbell’s (2001) neutral theory of communities suggests that many ecologists were willing, after struggling for decades without resolving the diversity problem, to entertain theories that discount ecological interactions and niche specialization completely. Hubbell’s theory is historical and geographical (*geohistorical*). Diversity depends solely on the area of suitable habitat within a region (that is, proportional to the number of individuals in the metacommunity) and the rate of species production, assuming that systems have had sufficient time to attain equilibrium. Species extinction is purely stochastic, depending only on the size of a population. The theory includes ecology only in the sense that the total number of individuals within the regional metacommunity is fixed. Thus, all individuals compete on a homogeneous ecological landscape, but on equal footing irrespective of their identity. As species richness within the metacommunity increases, average population size decreases, as does the time to extinction. This balances species production to arrive at the equilibrium diversity.

Although a purely neutral theory does not withstand scrutiny on a number of counts (Chave 2004), particularly because neutral drift is too slow to account for the development of ecological patterns (Ricklefs 2006a), a purely local, ecological theory of diversity also cannot account for certain empirical patterns. These include correlations between local and regional diversity (Cornell and Lawton 1992, Srivastava 1999), which contradict the idea of local saturation of species richness, and incomplete convergence in diversity between areas of similar environment in different regions with independently evolved biotas (e.g., Latham and Ricklefs 1993a, Qian and Ricklefs 2000).

A geohistorical, evolutionary alternative to both local determinism and neutral theory is the generation of gradients of species richness through diversification within ancestral *ecological zones of origin* combined with occasional adaptive shifts associated with invasion of new ecological zones (Farrell et al. 1992, Latham and Ricklefs 1993b, Wiens and Donoghue 2004). The idea presumes that species are best adapted to the conditions in the ecological zone of origin of their lineage;

transitions to other ecological zones require evolutionary change. This evolutionary model establishes gradients of diversity, producing greater species richness in environments that are older, more widespread, or less stressful. The idea originated with biogeographers (e.g., Darlington 1957, Axelrod 1966), but was slow to be adopted by ecologists. Terborgh (1973) was the first to articulate a comprehensive theory of community diversity that explicitly included historical and geographic influences on local species richness. Applied, for example, to the species richness of forest trees, the latitudinal gradient could be explained by the origination and diversification of most flowering plant lineages in the extensive tropics of the early Tertiary (Burnham and Johnson 2004, Davis et al. 2005), followed by diversification of some lineages across adaptive barriers into high-latitude frost zones (Latham and Ricklefs 1993*b*). This process is shown diagrammatically in Fig. 1.

A second evolutionary alternative to local determination is that rates of evolutionary proliferation of species (speciation minus extinction) are higher in regions or ecological zones of high diversity (Farrell and Mitter 1993, Jablonski 1993, Cardillo 1999). This mechanism could be called a general process if certain ecological conditions, such as temperature, promoted or retarded proliferation (Rohde 1992, Allen et al. 2002), or a special process if proliferation depended on unique physiography or geographic configurations of regions or if extinction depended on unique history. For example, Qian and Ricklefs (2000) speculated that the high diversity of plants in temperate eastern Asia could be related, in part, to the complex physiography of the region, which is both mountainous and features land masses (China mainland, Korean peninsula, and Japan) that have alternately been connected and separated as sea levels have risen and fallen during the Tertiary. Molecular phylogenetic analysis of plant clades distributed in eastern Asia and North America supports both an older age (Asian taxa paraphyletic to North American taxa) and more rapid diversification in eastern Asia as underlying causes of diversity differences (Xiang et al. 2004). Extinction also can play a role (Vermeij 1987, Jablonski 1991). For example, Latham and Ricklefs (1993*a*) and Svenning (2003) concluded from comparisons of fossil and modern taxa that the impoverished tree flora of Europe resulted from differential extinction of species within predominantly tropical and subtropical groups caused by cooling climates and glaciation during the late Tertiary.

#### THE INFLUENCE OF LOCAL AND REGIONAL PROCESSES

If one accepts the premise that local diversity represents a balance between the constraining influence of local population interactions and the augmenting influence of regional species production, then one can hope to estimate only the relative balance of these factors in determining patterns of species richness. Moreover, general and special processes often make

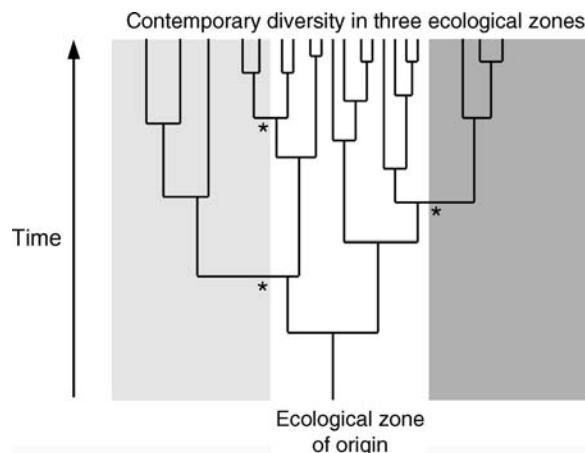


FIG. 1. Evolutionary diversification of a clade within its ecological zone of origin, with occasional adaptive shifts (stars) to different ecological zones. The adaptive shifts might be difficult and occur infrequently, potentially establishing a gradient in contemporary diversity that favors the ecological zone of origin. Modified from Ricklefs (2005*a*); see also Wiens and Donoghue (2004).

the same predictions, which cannot then be used to distinguish between them. For example, if species richness were determined locally by ecological constraints on species packing, the phylogenetic history of the species in regions having different diversity might also be consistent with a diversification constraint.

A simple classification of the mechanisms that influence diversity is presented in Table 1. These are divided into local and regional/historical processes, and the latter are further subdivided into the influences of the ecological zone of origin, of environment on the rate of diversification, and of diversity itself in promoting or retarding further diversification.

#### Community saturation

Taken to its extreme, local determinism predicts that communities are saturated with species and that species richness is directly related to factors in the physical environment that determine the number of species that can coexist locally (Table 1: Panel A). Community saturation implies an upper limit to the number of species in a local assemblage, regardless of the diversity within the surrounding region (Cody 1966). In principle, this hypothesis can be confirmed in comparisons of species assemblages in the same habitats between areas having different regional diversity, i.e., the principle of community convergence (e.g., Oriens and Paine 1983, Schluter and Ricklefs 1993), particularly when local diversity levels off with increasing regional diversity. Terborgh and Faaborg (1980) were the first to apply a saturation test explicitly, with a positive result. Most subsequent studies have failed to find evidence for a hard upper limit to species number, but Srivastava (1999) called attention to the shortcomings of such analyses, including inconsistent definitions of local and

TABLE 1. A classification of influences on large-scale patterns in local diversity.

Mechanism	Comments
A) Local determinism	Explanations based on local factors require explicit models of how the physical environment influences coexistence.
a) Limiting similarity and saturation	This extreme form of local determinism predicts community convergence, which is rejected in many comparative studies.
b) Diversity increases resistance to invasion	Ecological compression and release demonstrate the influence of population interactions on local community membership.
B) Regional/historical processes	These models predict diversity within larger regions, but also provide external drivers for local species richness.
a) Ecological zone of origin	Phylogenetic analysis permits the reconstruction of ancestral ecological positions within the environmental landscape.
i) Age and area	Phylogenetic analysis provides an estimate of relative age; area effects are apparent in contemporary biotas, but the relative roles of species production and extinction should be distinguished.
ii) Adaptive diversification	Zones of origin can be identified by phylogenetic analysis, and these should support the highest species richness regardless of the depth of the clade stem.
b) Net rate of diversification	Differences in rates of diversification can be seen in lineage-through-time plots and inferred, to some degree, from genetic distances between sister taxa.
i) Physiography and history promote speciation	Assuming allopatric speciation, regional analyses of geographic heterogeneity at appropriate scales would be informative, as would studies of incipient species formation (e.g., genetic differentiation of populations)
ii) Climate change and catastrophes cause extinction	This can be judged primarily through analysis of fossil material and the geological record, hence applications are limited to groups with good fossil records.
iii) Diversity promotes or retards diversification	Diversity might be self-accelerating or self-limiting. The pattern is accessible through analysis of lineages through time and analysis of biological and physical aspects of niche structure in contemporary biotas.

regional scales and lack of independence between regions. Ricklefs (2000) emphasized the balance between local and regional factors, pointing out that increased "regional" diversity among West Indian island avifaunas was accommodated equally by increases in local species richness and turnover of species between habitats. Consistent with this ecological flexibility, introduced species apparently have not caused extinctions on islands through competitive exclusion (Sax et al. 2002; but see Gurevitch and Padilla (2004)), and establishment of new colonists in the avifauna of the Lesser Antilles appears to be independent of local diversity (Table 1, [Panel B, row b(iii)]; Ricklefs and Bermingham 2001). Over longer periods observable in the marine fossil record of the Paleozoic Era, for example, diversity does appear to have constrained diversification (e.g., Foote 2000).

#### *Local constraint*

Local constraint predicts that local species richness should be strongly correlated with environmental conditions, irrespective of the mechanisms regulating coexistence. Under local determinism, diversity patterns must ultimately be related to physical aspects of the environment (e.g., Ricklefs 1977, Currie et al. 2004). Many studies have demonstrated strong correlations between local species richness, using various definitions of the scale of "local" (Rahbek and Graves 2001, Willis and Whittaker 2002), and climate (Currie 1991, O'Brien 1998, Hawkins et al. 2003b) or other variables, such as habitat structure (Cody 1974) and productivity (Rosenzweig 1995, Mittelbach et al. 2001). Coefficients of

determination commonly fall in the range of 60–70%, or more (Hawkins et al. 2003a). However, such correlations might also be predicted by evolutionary theories of species richness patterns, where diversity reflects either environmental history combined with evolutionary inertia, or the influence of environment on net species proliferation.

#### *Unique history and geography*

Local constraints predict convergence of local community properties in similar environments regardless of the evolutionary and geographic history of a region, within which species richness might vary widely. Conversely, differences in species richness in the same habitat between regions suggest that special factors influence local assemblages. Such differences have been noted frequently in community comparisons. Among the most conspicuous of these *diversity anomalies* in plants, for example, are the difference in species richness between mangrove communities in the Indo-West Pacific and the Atlantic/Caribbean regions (Duke 1992, Ricklefs and Latham 1993), the depauperate tree flora of Europe compared to eastern Asia (Latham and Ricklefs 1993a), and the greater diversity within disjunct genera of angiosperms in eastern Asia compared to eastern North America (Qian and Ricklefs 1999). Such diversity anomalies have been explained by differences between regions in (a) the frequency of adaptive shifts of new lineages to the stressful mangrove environment, (b) extinction in the case of the European tree flora, and (c) a combination of species production, species invasion from the tropics, and late-Tertiary extinction in the case

of the disjunct temperate floras of Asia and North America. Although special explanations for diversity anomalies make good sense, they are suggested by the data themselves rather than emerging from the use of data to test contrasting predictions. Special explanations are difficult to place in an experimental or hypothesis-testing framework (Francis and Currie 1998), and the anomalies themselves might reflect unmeasured differences in local environments between regions (Pianka 1975, Morton 1993, Ricklefs et al. 2004).

Can diversity anomalies be used other than to provide anecdotal support for the idea of special influences on diversity? Some special geographic circumstances are repeated themes in many regions of the world. Among terrestrial environments, for example, mountainous areas coincide with diversity hotspots (e.g., Barthlott et al. 1996, Orme et al. 2005), providing an opportunity to test the consistency of some special relationships. Even where these relationships are unique, geographic/historical models suggest mechanisms, such as enhancement of allopatric speciation or restriction of evolutionary diversification, which can be assessed in multiple, independently evolving lineages. Thus, although empirical observations might not provide statistical support for a particular historical scenario, one might obtain statistically valid appraisals of mechanisms postulated to be at work within a unique geohistorical framework.

#### *Speciation rate*

The role of speciation rate in creating patterns of diversity (Table 1, [Panel B, row b]) has received considerable attention, particularly with respect to identifying the influence of “key innovations” on diversification (Slowinski and Guyer 1993, Heard and Hauser 1995, Bennett and Owens 2002). Among the more successful of these tests have been the association of rapid diversification in insects with the switch to herbivorous diets and the association of rapid diversification in plants with the evolution of certain defenses against herbivory (Farrell and Mitter 1994). The physiography of particular regions, such as eastern Asia, might promote species production. General characteristics of the environment, such as the benign nature of tropical climates, could also influence speciation rate (Dobzhansky 1950, Schemske 2002). Several authors have suggested that thermal energy can accelerate speciation (e.g., Rohde 1992, Allen et al. 2002). Attempts to test hypotheses on the rate of speciation have focused on comparisons of sister (same-age) clades in tropical and temperate regions (Farrell and Mitter 1993, Cardillo 1999, Cardillo et al. 2005, Ricklefs 2005*b*, 2006*b*), but these have been relatively inconclusive because suitable data are difficult to assemble. Such comparisons depend on well-supported phylogenies. Because these are rapidly increasing in number, testing the effect of various environmental or regional factors on rates of species production will become more commonplace and will show whether and how speci-

ation rate and the ages of lineages influence diversity within regions (e.g., Xiang et al. 2004).

#### *Ecological zone of origin*

Every lineage of organism has an ecological zone of origin (Table 1 [Panel B, row a]), which, under some circumstances, can be identified by tracing character (i.e., ecological zone) evolution on a phylogenetic tree (e.g., Schluter et al. 1997). This is similar to inferring the geographic area of origin, which often can be ambiguous (Ronquist 1997, Brown and Lomolino 1998:Chapter 12, Sanmartin et al. 2001). When an entire clade is restricted to a particular ecological zone, one can infer that it originated within that zone, even though this parsimonious conclusion might be incorrect (Davis et al. 2005). When a clade is distributed over several ecological zones, identifying the origin in the absence of fossil evidence depends on the paraphyletic distribution of zones over the clade.

#### *Diversification across adaptive barriers*

Some of the strongest diversity gradients are clearly associated with particular environmental stressors (Table 1 [Panel B, row a(ii)]), including high salt and substrate anoxia in the case of mangrove vegetation and freezing in the case of temperate vegetation. The roughly 20 present-day lineages of mangrove trees and shrubs were independently derived from terrestrial lineages of plants over a period of more than 60 million years (Ricklefs and Latham 1993, Ellison et al. 1999). This suggests that the evolutionary transition from terrestrial to mangrove environments is difficult and that this adaptive barrier is crossed infrequently. The same is likely true of evolutionary transitions from mesic tropical to temperate habitats (Terborgh 1973). Phylogenetic analysis reveals that the lineages of trees in north temperate latitudes are mostly nested within clades having deep tropical origins (Ricklefs 2005*a*). Indeed, more than half the families of flowering plants are restricted to tropical latitudes and evidently have not been able to cross the adaptive barrier into temperate latitudes (Ricklefs and Renner 1994). During most of the early evolution and diversification of the flowering plants, the planet's environments were predominately tropical (Behrensmeyer et al. 1992, Graham 1999).

Models of the establishment of regional patterns of species richness, based on origins vs. rates of proliferation, can be distinguished by phylogenetic analysis (compare Figs. 1 and 2). Whether either of these evolutionary models were to shape gradients in local diversity, in contrast to merely reflecting the gradient in numbers of contemporary coexisting species permitted by ecological interactions, is more difficult to resolve. That is, all species have an evolutionary history, including relationships to other lineages, and one can reconstruct phylogenies for the members of a local community regardless of the mechanisms that control local diversity. A role for adaptive barriers can be

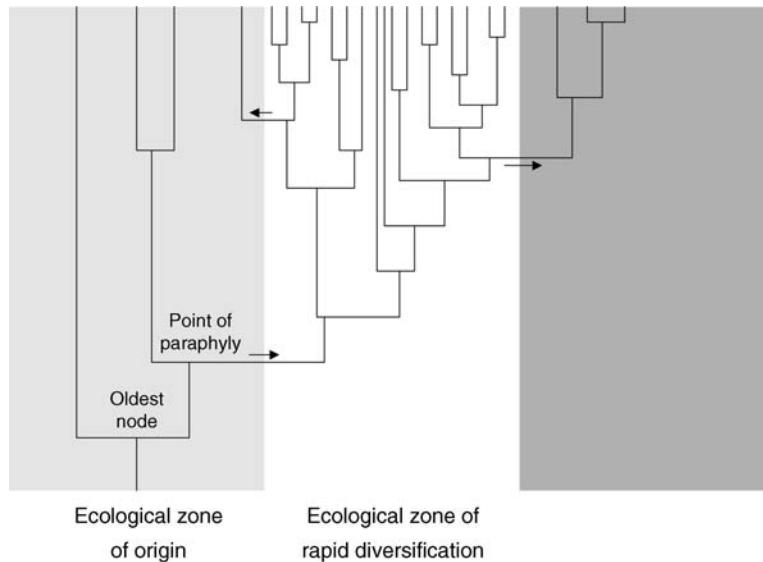


FIG. 2. When species proliferate more rapidly in a novel environment than in the ecological zone of origin, diversity need not coincide with the ancestral environment. In this example, the zone of origin can be identified through phylogenetic analysis, because species within the ancestral zone are paraphyletic with respect to species in the zone of highest diversity.

inferred from the partitioning of evolutionary lineages between ecological zones (Webb 2000, Webb et al. 2002). If species can cross between these zones easily, ecological zone itself would be labile, varying at a shallow depth within a phylogeny, as in the case of oak species across a moisture gradient in Florida (Cavender-Bares et al. 2004) or evolutionary transitions to chaparral environments in western North America (Ackerly 2004). However, if these adaptive shifts were difficult, as in the case of entering the mangrove environment, ecological zone would appear to be a conservative trait. For example, the four genera and perhaps 17 species of mangrove Rhizophoraceae represent a single lineage that entered the mangrove environment early in the evolution of the family and diversified there without any lineages crossing back to the terrestrial ecological zone (Schwarzbach and Ricklefs 2000).

#### PROSPECTS

Ecological regions of high diversity and ecological regions of origin likely coincide, although rates of lineage proliferation also appear to differ between regions and might produce a contradictory pattern (Fig. 2). In general, ecological and evolutionary models for the origin and maintenance of diversity gradients cannot be distinguished by examining patterns of diversity. Because of this, ecologists must expand their inquiries to include evolutionary hypotheses (Webb et al. 2002, Ackerly 2004), and they must develop mechanistic, testable, ecological models that connect diversity to the physical environment (Currie et al. 2004).

Special explanations for species richness require that special processes have strong enough influence to leave a distinctive imprint on ecological pattern. Evolution and

adaptation are slow compared to local ecological dynamics. However, when the interactions between species play out within regions rather than local communities, general processes can adjust ecological and geographic distributions of species so that all populations come into demographic balance within the region (Ricklefs 2004). Ironically, this deterministic outcome is independent of special aspects of regions and lineages, including the number of species that have been generated within a region. As more species are added, ecological distributions are compressed, beta diversity (species turnover with respect to ecology and distance) increases, and equilibrium is maintained (Terborgh 1973). This concept requires that ecologists consider populations as regional ecological entities made integral by the movements of individuals (Lennon et al. 1997, Ricklefs 2004, Case et al. 2005, Holt et al. 2005).

Evolutionary and geographic history—special components of ecological systems—can be revealed through phylogenetic analysis, among other approaches, which provides insight into the development of diversity patterns and unique aspects of biological communities in different regions. Speciation and extinction also reflect the intimate connections between ecology, geography, and evolution. Although many areas of ecological inquiry are independent of evolution and history, interactions between species played out within a large regional context bring ecological and evolutionary processes onto a continuum of scale that intimately links local ecology, history, and geography. Within this regional context, ecologists can characterize species distributions, including sampling on a variety of scales that comprise local individual movements, population interactions, habitat heterogeneity, and regional pro-

cesses of population subdivision and species formation (Rahbek 1997, Rahbek and Graves 2001). Islands, particularly archipelagoes, will continue to be important laboratories for studying mechanisms of species origination (Grant 1998, Mayr and Diamond 2001) and the response of ecological distributions to the pressure of regional diversity (Cox and Ricklefs 1977). Analyses of the niche structure of assemblages, particularly by defining the multivariate dimensionality of niche axes from ecological, morphological, and life history data (Ricklefs and Miles 1994), will assess the contribution of niche space to diversification and the complementary contribution of niche diversification to the evolutionary development of species assemblages. Most of these techniques are familiar to ecologists; new directions for the future will arise from their application in a novel framework.

Within this framework, I can make several specific recommendations. Of course, this list reflects my own perspective and would be broadened considerably by others. First, it is important to understand that the scale of analysis must be appropriate to the scale of the process in both time and space. Thus, if one accepts the premise that regional and historical processes can influence the development of local assemblages of species, then analyses of patterns of local diversity must include regional distribution and both environmental and evolutionary history. These might be accommodated, in part, in the following ways.

1) It is essential that ecologists abandon the idea of the local community. Interactions occur between populations over large regions, and we should therefore characterize the distributions of species on the geographic and ecological gradients over which they interact (Case et al. 2005). What ecologists have traditionally regarded as a "community" comprises the populations that co-occur together at a particular point in these regional continua of conditions. Whittaker (1967) and others used this approach in gradient analysis of vegetation. Sampling is conducted in plots along environmental gradients, and species populations can be characterized by their mean position, dispersion, and modal abundance along these gradients. When gradients are made comparable between regions, differences in the overlap and partitioning of species along these gradients can be compared as an approach to understanding how population responses accommodate variation in region diversity (e.g., Nekola and White 1999, Qian et al. 2005). Although this will be straightforward in principle, it may be difficult in practice because ecologists typically consider too few large-scale gradients within regions to separate hundreds or thousands of species. Ordination and canonical correspondence analysis typically explain a modest proportion of the variance in species distributions, leaving the rest to biological complexities in the environment and chance, both of which have traditionally been ignored by ecologists (cf. Condit et al. 2002).

2) The history of distribution of clades over environmental gradients involves adaptive changes and may constrain the diversity of species. Accordingly, it is important to examine patterns of species richness across environmental gradients in a phylogenetic framework. The general context for this is presented in Figs. 1 and 2. Ecologists should focus on strong barriers (e.g., frost tolerance, salinity gradients) as well as less imposing temperature and moisture gradients within regions (Ackerly 2004, Cavender-Bares et al. 2004). Such studies should seek factors that influence multiple lineages and that presumably impose the strongest constraints. These analyses of habitat shifts should be based on well-supported phylogenies, preferably in which branch points can be dated by fossils or calibrations developed for other lineages (e.g., Kishino et al. 2001, Renner and Meyer 2001) to relate adaptive shifts to climate or geographic change, and they must also use proper estimates of ancestral environments (Schluter et al. 1997). Although this approach is primarily descriptive rather than hypothesis testing, it can provide support for the prediction from adaptive constraint that ancestral lineages might change abruptly at a deep level across strong environmental gradients (Westoby 2006).

3) Building upon the analysis of population distributions within regions and phylogenetic analysis across environmental gradients, it seems reasonable to examine local assemblages and distributions of species across particularly important gradients of diversity. Among these, one that has been important in development of ideas about species richness patterns is the difference in tree species diversity between tropical and temperate environments. The transitions between these ends of an environmental continuum for broad-leaved trees are located in areas (eastern Mexico, southern China) for which few floristic data exist, but where we might expect the greatest information concerning diversity gradients. Although altitudinal gradients do not have the same seasonal dimension as latitudinal gradients, they are also informative to the extent that species turn over in parallel fashion.

4) Several studies have examined the depth of the clades that comprise a community as a way to assess the relationship between the ages of lineages and their diversity. Simply put, if the net rate of diversification (speciation minus extinction) is homogeneous, older lineages will leave more descendants. That is, the logarithm of the number of species is a function of the net rate of diversification and time. Ricklefs and Schluter (1993) showed that the clades that comprised avian assemblages in a tropical locality in Panama were roughly twice as old as the clades that made up an assemblage in Illinois, based on field data in Karr (Karr 1971) and lineage ages from Sibley and Ahlquist (1990). The implication is that time is an important factor in both regional and local diversity. Hawkins (2005) has provided a more comprehensive analysis that shows the same pattern in the birds of Australia, and Ricklefs

(2005a) confirmed the conventional botanical wisdom (Judd et al. 1994) that temperate trees belong to clades that are nested within deeper clades of tropical lineages. This topology is illustrated in Fig. 1, where the species in the more diverse ecological region belong to clades that have diversified within that region for longer periods.

5) A second facet of the historical dimension is the rate of diversification of species. All other things being equal, diversity increases as a function of the rate of diversification and time (Ricklefs 2006b). Thus, faster diversification leads to more species over a given period. Although few studies have made this comparison to date, and these have been inconclusive, the increasing availability of phylogenetic reconstructions will change this prospect rapidly. Appropriate comparisons include sister clades that occur in different regions or environments (Farrell and Mitter 1993, Cardillo 1999), which, by definition, are of equal age, or samples of clades from different regions or environments for which age and number of taxa are known (e.g., Cardillo et al. 2005, Ricklefs 2005b). Another approach is the lineage-through-time plot (Nee et al. 1992, Harvey et al. 1994), whose slope can be used, with well-sampled phylogenetic reconstructions of large clades, to estimate both speciation and extinction rates (e.g., Ricklefs 2006a). Another index to the rate of species proliferation is the genetic divergence between sister species, which in general decreases as the rate of speciation increases and extinction decreases. In all aspects of analyses that address species properties, results depend on the way in which species are defined, which should be as uniform as possible across comparisons.

6) Speciation as a process contributing to regional diversity can be examined phylogeographically by searching for incipient speciation among geographically separated populations. Incipient species might be recognized by large genetic differences between populations (Avice 2000), but, in any event, these can be compared easily among regions in terms of the number and geographic distribution of populations or subpopulations at a particular phylogenetic depth (e.g., Brumfield and Caparella 1996, Bates et al. 1999, Weir and Schluter 2004). This type of analysis could identify regions of rapid population differentiation that might lead to high rates of species production. Diversity is built up locally only when geographically isolated, evolutionarily independent populations achieve secondary sympatry. Thus, comparison of sister taxa in allopatry and sympatry (assuming an allopatric model of species formation), would permit an analysis of the time required for the local accumulation of species and whether the ecological differentiation that permits coexistence evolves in allopatry, or primarily by divergent selection after the initiation of secondary sympatry. Island groups, with their discrete geographic organization, provide ideal opportunities for exploring these issues (Grant 1998, Ricklefs and Bermingham 2001).

7) Finally, extinction can play an important role in the establishment of patterns of diversity. Where an adequate fossil record exists, one has a direct estimate of diversity, at some resolution, through time. The extinction of many clades of animals at the Cretaceous–Tertiary boundary, as well as the disappearance of many plants from Europe during the late-Tertiary period of climate cooling (Sauer 1988, Latham and Ricklefs 1993b, Svenning 2003), provide instructive examples of the importance of this factor. A large literature in paleontology addresses rate of extinction and its relationship to diversification, environmental changes, catastrophic events, and changes in the configurations of landmasses and ocean basins (Jablonski 1989, 1991, 1993, Vermeij 1991, Jackson et al. 1993). Unfortunately, the fossil record is rarely resolved to the taxonomic level of species and hardly exists for many groups. This should not prevent those of us interested in living forms from examining what is known of the fossil history of a group. At some level of resolution, this will provide at least an envelope around possible historical scenarios. Where fossil data are not available, information can be extracted from models of lineage diversification (e.g., Magallón and Sanderson 2001, Ricklefs 2006a) and extinction inferred, for example, from gaps in the distribution of species through archipelagoes (Ricklefs and Cox 1972, Ricklefs and Bermingham 1999).

The better we develop the space and time contexts of ecological systems, the more we shall appreciate the variety of factors that have influenced their composition and diversity. We should view populations as evolved entities, with unique histories and adaptations, that are distributed geographically according to their tolerance of ecological conditions and interactions with other populations, and, within the limitations of dispersal, over regional landscapes. Inevitable consequences of these processes are the co-occurrence of a unique assemblage of species at any particular point and geographic patterns in the number of species observed over many such points over the surface of the earth.

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