

A comprehensive framework for global patterns in biodiversity

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Abstract

The present study proposes to reconcile the different spatial and temporal scales of regional species production and local constraint on species richness. Although interactions between populations rapidly achieve equilibrium and limit membership in ecological communities locally, these interactions occur over heterogeneous environments within large regions, where the populations of species are stably regulated through competition and habitat selection. Consequently, exclusion of species from a region depends on long-term regional-scale environmental change or evolutionary change among interacting populations, bringing species production and extinction onto the same scale and establishing a link between local and regional processes.

Keywords

Beta diversity, community, competition, diversity, extinction, habitat breadth, local processes, regional processes, speciation, species richness.

Ecology Letters (2004) 7: 1–15

INTRODUCTION

Large-scale patterns of taxonomic diversity have challenged biologists ever since Europeans took natural history exploration to the far corners of the globe in the 18th and 19th centuries. These patterns have stimulated more explanations and hypotheses than one can reasonably test with the data at hand (Pianka 1966; Huston 1979; Rohde 1992; Huston 1994; Rosenzweig 1995; Ritchie & Olff 1999; Colwell & Lees 2000; Dynesius & Jansson 2000). Being unable to reject hypotheses easily, and faced with the likelihood that many processes influence patterns of diversity, biologists understandably hold divergent views on this issue. Prior to c. 1960, most ideas about diversity were founded in history and geography. Diversity was believed to rise to its fullest extent through evolutionary diversification over long periods within large areas. The unification of population biology and biogeography in the 1960s, most famously by Robert MacArthur and his associates and students (MacArthur 1965, 1972), brought diversity into the ecological back yard. New theories maintained that membership in ecological communities was limited by interactions among species – broadly, competition, predation, and mutualism. These interactions, which played out within small areas over ecological time, provided a basis for understanding diversity patterns. As the historian of science, Sharon Kingsland (1985), put it, community ecology ‘eclipsed’ history, to the point that in

many minds the two were incompatible. Ecologists and population biologists largely supported explanations for diversity patterns based on species interactions within communities; systematists and biogeographers were reluctant to abandon historical explanations, but mostly remained in the background (see Whittaker 1972; Rosenzweig 1975, 1978; Connor & Simberloff 1979).

Three issues aggravated this division between historical and ecological approaches to diversity patterns. First, historical hypotheses were considered by many to be untestable and thus not valid scientific hypotheses (e.g. Francis & Currie 1998). Second, experimental and model systems demonstrated that ecological interactions ran to steady-state conditions too rapidly for slower evolutionary processes to have a local impact (Pielou 1977). Third, strong correlations between diversity and local ecological conditions were consistent with the idea that local interactions constrain diversity, and they therefore seemed to provide a sufficient explanation (Turner *et al.* 1987; Currie 1991; Wright *et al.* 1993; Lennon *et al.* 2000; Whittaker & Field 2000). The continued interest in diversity patterns and the instability of ideas about their causes – witness the flurry of interest recently over Hubbell’s (2001) neutral theory of ecological communities (Zhang & Lin 1997; Yu *et al.* 1998; Abrams 2001; Bell 2001; Brown 2001; Chave *et al.* 2002; Cody 2002; Condit *et al.* 2002; Ricklefs 2003a; Volkov *et al.* 2003) – reflects the prominence of diversity as a bellwether of our understanding of ecological systems.

Here I outline a potential resolution to the diversity impasse that brings together diverse ideas with long tenure in the literature of ecology and biogeography. My rationale is simply that the local and regional mechanisms that influence diversity interact on a continuum of time and space, which both creates a regional effect on diversity and establishes a relationship between regional and local diversity. The basic idea is that interactions among coexisting individuals influence change in population size locally. However, because of the dispersal of individuals through populations, these interactions are played out over large, environmentally heterogeneous regions rather than within local 'communities' in relatively uniform habitats. Changes in the relative success of populations caused by the evolution of biotic interactions, perhaps particularly those between parasites or pathogens and their hosts, are expressed as variations in geographical and habitat distributions. These distributions are mutually adjusted to the point that at any one time all populations are more or less stably regulated. Extinction within such large regional assemblages of populations can only result from persistent changes in climate and landforms or from evolutionary changes in populations of food resources, competitors, predators, and pathogens. As these changes are slow, waiting times to extinction are of the same order of magnitude as the production of new species, bringing species loss and species production into the same time range. Thus, large-scale regional processes influence regional diversity, and regional and 'local' diversity are directly connected.

A BRIEF HISTORY OF THE DIVERSITY ISSUE

Contemporary thinking about diversity patterns has drawn upon many sources over more than a century. This history provides the foundation of our contemporary framework for diversity analysis and interpretation. Biologists have long recognized many patterns of diversity, particularly those relating species richness to area, latitude, habitat productivity and isolation on islands or peninsulas (McIntosh 1985, p. 140; Huston 1994; Rosenzweig 1995). Throughout most of the 19th and 20th centuries, explanations for these patterns centred upon large-scale processes occurring over long periods and large areas (Willis 1922), emphasizing the relative stability of the tropics (Wallace 1878) and the more rapid evolution and species production in tropical environments (Fischer 1960), perhaps stimulated by their higher temperatures and more complex and intense biotic interactions (Dobzhansky 1950; Janzen 1970). Until the 1960s, however, ecologists had little to say about patterns of diversity. Indeed, the topic was rarely mentioned in ecology texts published before 1970.

By the mid-1960s, population processes had become fully integrated into the burgeoning discipline of community

ecology, and the realization that interactions among coexisting species could constrain their number shifted thinking about diversity dramatically. This change was the culmination of a long tradition of population biology starting in the 1920s and 1930s with the development of population models (Volterra 1926; Pearl 1927; Lotka 1932) and microcosm experiments (Gause 1934). These studies led to the principle of competitive exclusion (Hardin 1960), which was extended to natural communities, building on Elton's (Charles 1927, 1946) concept of food webs and community membership, by David Lack's studies of ecological isolation (Lack 1944) and adaptive radiation (Lack 1947). From these beginnings, Hutchinson (1957, 1959) developed basic aspects of niche theory and asked how species were able to coexist in communities. The theory of competition and limiting similarity was developed by MacArthur & Levins (1967) and extended by others to the stability of community matrices representing the interactions of species within communities (Vandermeer 1969, 1972; May 1975). The community matrix provided an objective way of assessing how successfully species could invade communities and the ability of species interactions to limit community membership (Moore *et al.* 2001; Shurin & Allen 2001; Mouquet *et al.* 2002). The idea that interactions limit coexistence (community saturation) led Diamond (1975) to propose assembly rules for communities (Fox 1987; Fox & Brown 1993; Weiher & Keddy 1995; Belyea & Lancaster 1999; Kelt & Brown 1999; Weiher & Keddy 1999; Brown *et al.* 2000), which conveyed the impression that community development would lead to an inherently stable structure (but see Petraitis *et al.* 1989; Petraitis & Dudgeon 1999; Huisman & Weissing 2001, concerning alternative stable communities).

The community ecology revolution fostered the idea that membership in communities was limited by species interactions and that these interactions could explain patterns in species richness. By this time, ecologists had fully assimilated the problem of species diversity. Although they recognized that the number of species in large regions might be influenced by large-scale processes or by unique historical events, disparity between local and regional diversity could be accommodated by variation in the turnover of species between habitats within regions, also known as beta diversity (Whittaker 1972; Cody 1975). Thus, for example, the Tertiary increase in the taxonomic richness of marine organisms (Raup 1972), land plants (Knoll 1986), and probably many other groups could be accommodated within the framework of locally determined diversity by increased spatial turnover, or regionalization, of biotas (Marshall *et al.* 1982; Sepkoski 1988; Webb 1989; Van Valkenburgh & Janis 1993).

The rise of local determinism was helped along by the results of models and microcosm experiments showing that

local interactions run to equilibrium quickly, generally within a few tens of generations (Ricklefs 1989). Larger regional processes responsible for the production of new species (speciation, immigration from elsewhere) are much slower. Even where species formation is rapid (e.g. following hybridization and allopolyploidy; Stebbins 1974; Grant 1981), such events are infrequent. Thus, large-scale processes were considered too weak to influence local equilibria achieved by local processes.

Local determinism implies that patterns of diversity reflect attributes of the physical environment that influence the outcome of species interactions. Moreover, communities with independent evolutionary histories but occupying similar physical environments should exhibit local convergence in community properties, including species richness (Cody & Mooney 1978; Orians & Paine 1983; Schluter & Ricklefs 1993). Thus, local determinism makes three predictions: (1) diversity should be strongly correlated with physical aspects of the environment; (2) local diversity in comparable habitats should not vary between regions; (3) local diversity, at least above some ecological saturation level, should be independent of regional diversity.

Considering these predictions, the construction of diversity theory on a foundation of local determinism was ironic in two respects. First, this came at a time when ecologists were struggling with competing views of communities as closed natural units (Clements 1936) vs. open structures without absolute boundaries (Gleason 1926). Although the issue was settled on the side of mostly open community structure through the work of R. H. Whittaker and others (Whittaker 1953, 1967; McIntosh 1985), the community models and experimental microcosms upon which ecological diversity theory rests are basically closed structures with well-defined boundaries (Roughgarden 1989). Second, as the idea of local determinism was strengthening its hold on diversity theory, MacArthur & Wilson (1963, 1967) developed their famous equilibrium theory of island biogeography, in which a strong external influence (colonization from source areas) drives patterns in island diversity.

To be sure, ecologists' views of communities have expanded greatly since the 1960s to accommodate the connections between communities resulting from movement of individuals between patches of a particular habitat and between habitats. These innovations have included supply-side ecology (Roughgarden *et al.* 1987), metapopulation dynamics (Hanski & Gilpin 1997), landscape ecology (Turner *et al.* 2001), mass effects (Shmida & Wilson 1985), source-sink relationships (Pulliam 1988), Rapaport's rule (Stevens 1989) and macroecology (Brown 1995; Maurer 1999; Gaston & Blackburn 2000). Spatial considerations now play a prominent role in the development of theory concerning the outcome of interactions between species and

the maintenance of community stability (Chesson 2000; Shurin & Allen 2001; Holt 2003; Morris 2003). Nonetheless, these developments remain tied to the idea of a local equilibrium dependent on the unfolding of population processes within a complex, heterogeneous setting.

TESTING LOCAL DETERMINISM

Of the three predictions attending the idea of local determinism, prediction 1, that diversity should parallel variation in the physical environment, has garnered the most evidence (Wright *et al.* 1993). Analyses of the diversity-environment relationship typically employ climate variables (temperature, precipitation) to describe the physical environment, including derived variables related to energy input (e.g. potential evapotranspiration) or total water flux (e.g. actual evapotranspiration), and seasonality in these variables (O'Brien 1993, 1998; Currie *et al.* 1999; Francis & Currie 2003). The spatial scales of such comparisons are sometimes local, but more often involve diversity within large sampling areas based on latitude-longitude grid cells. Coefficients of determination usually exceed 60% and often exceed 80% (e.g. Fraser & Currie 1996; Kerr *et al.* 1998; Francis & Currie 2003). Additional information might be carried by other environmental variables including soils, topography and heterogeneity within sample areas (e.g. Huston 1980; O'Brien *et al.* 2000; Rahbek & Graves 2001), but these are less frequently included in analyses.

Although many ecologists have used diversity-environment correlations to support the idea of local determinism (Currie *et al.* 1999), several considerations weaken this interpretation. Most critically, the diversity-environment relationship can result from evolutionary models of diversification as well as from diversity limitation by ecological interactions (Farrell *et al.* 1992; Latham & Ricklefs 1993b). All clades diversify from a single ancestral lineage that occurred in an ecological zone of origin. If one assumes that adaptive shifts to other ecological zones are constrained (Ackerly 2003), or that rates of diversification differ among ecological zones (Jablonski & Bottjer 1990, 1991; Jablonski 1993), then a diversity gradient between ecological zones will persist over time. Considering that most of the land surface of the earth was tropical or subtropical throughout much of the Tertiary (Behrensmeyer *et al.* 1992), it would not be surprising if the greater diversity in the present-day tropics were an outcome of historical/evolutionary processes (Crane & Lidgard 1990). For example, the diversity-environment relationship for plant clades that diversified in extratropical latitudes (e.g. Manos & Stanford 2001), including, by one estimate, more than 50 families of flowering plants (Ricklefs & Renner 1994), would differ substantially from that for flowering plants in general, reflecting their evolutionary origin and diversification within

temperate ecological zones and their failure to adapt subsequently to warmer zones.

A second concern is that diversity–environment studies are generally confined to correlations and do not incorporate means of rejecting hypotheses about the ways in which the available niche space varies among, or is divided among, species inhabiting areas with different local diversity. Mechanisms governing the relationship of diversity to physical factors in the environment rarely are addressed directly (Ricklefs 1977). According to Currie *et al.* (1999), this is relatively unimportant compared with the formalism of erecting falsifiable hypotheses: ‘Mechanistic hypotheses that predict more than just patterns of richness would be desirable, but simple correlative hypotheses that make testable predictions about patterns of richness in nature are better than elegant mechanistic hypotheses that, in practice, make no predictions.’ It is important to recognize that correlations do not imply mechanism. Regardless of the association of diversity with climate, unless we understand how interactions between populations of trees result in 300 coexisting species per hectare in Amazonian Ecuador and one-tenth that many in the richest forests in eastern North America, we cannot understand the origin and maintenance of these patterns.

Most explanations based on climate relationships depend on the ability of the total productivity of the habitat to support individuals, hence species (the productivity hypothesis: Wright *et al.* 1993; Huston 1994; Mittelbach *et al.* 2001) or the physiological tolerance of organisms for low energy environments (the ambient energy hypothesis: Pianka 1966; Turner *et al.* 1987; Currie 1991; Kleidon & Mooney 2000). The latter theory is not incompatible with historical–evolutionary explanations for diversity patterns because tolerance of physical conditions is an evolved property of populations and clades. Hubbell’s (2001) neutral theory would relate diversity to gradients of metacommunity size (J_M) and speciation rate (v), neither of which is a local factor. Thus, I would argue that local determinism – as distinguished from the diversity–environment correlation – is a weak theory without falsifiable predictions.

The two remaining predictions arising from local determinism are not strongly supported. Local diversity is generally positively related to regional diversity (e.g. Terborgh & Faaborg 1980; Ricklefs 1987; Hugueny *et al.* 1997), contrary to prediction 3, although Srivastava (1999) and Loreau (2000), among others, have discussed many pitfalls of this test. The curvilinear relationship between local and regional diversity observed in some analyses (e.g. Ricklefs 2000) is consistent with an increasing resistance to the addition of species to communities as local diversity increases, implying a combined influence of local and regional processes.

Some authors, including Francis & Currie (1998), have suggested that prediction 2, which states that local diversity

in particular habitats should not vary between regions, is not testable because its rejection would depend on unique historical circumstances that cannot be independently verified. I believe that this position is untenable because explanations for contemporary pattern based on history are logically plausible and many historical or geographical factors, such as mass extinctions, the positions of islands near and far from sources of colonization, and the concentration of speciation in orogenic regions, are in fact repeated themes over the surface of the earth, which should have testable effects on diversity. Whittaker & Field (2000) argued that direct environmental determination should take precedence in explaining diversity patterns, and that regional and historical factors might be invoked to explain residual variation. I would argue instead that because the diversity–environment relationship can have a historical, evolutionary basis; neither type of explanation should be preferred at the outset. Where region effects on taxonomic richness can be demonstrated statistically, the burden of proof lies with advocates of local determinism to discover local environmental factors that can explain these differences through mechanisms that influence community membership. Merely assuming that such factors must exist is a weak position.

TESTING THE INFLUENCE OF REGIONAL PROCESSES AND HISTORICAL EVENTS

Even if one does not believe that prediction 2 can be rejected by comparisons between regions, the complementary prediction of regional effects – namely that diversity differs between comparable habitats in regions that have different histories or geographical configurations – can be rejected by the absence of a statistically significant region effect. However, where this prediction has been tested explicitly, regional effects are rarely rejected (Cody & Mooney 1978; Orians & Paine 1983; Latham & Ricklefs 1993a,b; Ricklefs & Latham 1993; Schluter & Ricklefs 1993; Fraser & Currie 1996; Kerr & Currie 1999). For example, both regional and local differences in tree species diversity between eastern Asia, eastern North America, and Europe clearly reflect the isolation of North America from Tertiary centres of tree diversification in Eurasia and rapid late Tertiary climate cooling in the disappearance of species from the flora of Europe (Sauer 1988; Latham & Ricklefs 1993a; Svenning 2003). When local, primarily deciduous tree floras ($10\text{--}10^4\text{ km}^2$) in temperate eastern Asia and eastern North America are matched by flora area and actual evapotranspiration in an analysis of covariance, the significant region effect is equivalent to a factor of 2, and exceeds variation among deciduous forest areas within each region related to climate (Latham & Ricklefs 1993b). Comparisons of diversity in genera that are disjunct between eastern Asia

and North America also strongly implicate regional factors, including the interaction of geography with climate and sea-level history to promote allopatric species formation, in causing diversity to differ between the two regions (Qian & Ricklefs 2000).

In a more striking example, the sixfold difference in the regional diversity of mangroves inhabiting comparable environments in the Indo-West Pacific and the Atlantic–Caribbean–East Pacific (Chapman 1976; Saenger *et al.* 1983; Duke 1992; Ricklefs & Latham 1993; Saenger 1998) scales down to a two- to threefold variation at the local (hectare) scale (Chapman 1976; Bunt *et al.* 1991). The western mangrove flora consists of older pantropical lineages (*Rhizophora*, *Avicennia*, *Laguncularia/Lumnitzera*, *Pelliciera*) that arose, probably in the Tethys region, during the early Tertiary (Ellison *et al.* 1999). Much of the diversity in the Indo-West Pacific comprises endemic forms whose first appearances in the fossil record are further to the east and more recent. Thus, historical data suggest that the regional diversity anomaly in mangrove plants is related to the relative facility with which terrestrial plants have invaded mangrove environments and diversified in the Indo-West Pacific region (Schwarzbach & Ricklefs 2000), perhaps because of the different configurations of landmasses and numbers of islands on continental shelves in the two regions. Although it may be difficult to prove such a historical scenario, the differences in diversity are real, in spite of the similarity in environment, and the historical/geographical hypothesis suggests potentially fruitful research on adaptive transitions between terrestrial and mangrove environments and species formation in mangroves. Other examples can be found in the influence of island size on within-island adaptive radiation and local diversity in *Anolis* lizards in the Greater Antilles (Losos & Schluter 2000), and the similar influence of allopatric speciation on adaptive radiation and island diversity in Darwin's finches in the Galápagos archipelago (Lack 1947; Grant 1986) and honeycreepers in the Hawaiian Islands (Amadon 1950; Fleischer & McIntosh 2001).

RECONCILIATION OF LOCAL AND REGIONAL PERSPECTIVES

If one (a) accepts the premise that diversity–environment relationships can arise historically, (b) allows that regional effects on local diversity cannot easily be rejected, and (c) sees that regional diversity anomalies are translated to the local level, then one is faced with the problem of having to reconcile the disparate scales of regional and local processes (Ricklefs 1989). In this context, two ideas that are ingrained in the ecological mind-set, whether we are conscious of them or not, have hindered the development of community ecology.

One is that local communities become ecologically saturated, at which point additional species cannot invade and diversity is capped (e.g. Diamond 1975; Terborgh & Faaborg 1980). This idea is an extension of the concept of a population carrying capacity, at which population size is regulated in a steady-state, by intraspecific, density-dependent competition among individuals. Replace individuals by species, and one has community saturation, i.e. carrying capacity. The idea of a steady-state is embodied in MacArthur & Wilson's (1967) equilibrium theory of island diversity, although no upper limit to species number is implied by this theory. The idea of saturation is tied to the concept of limiting similarity (MacArthur & Levins 1967), dictating the degree of niche overlap that can be tolerated by coexisting species. Although limiting similarity implies saturation in some interpretations of the theory, this is generally incorrect, except perhaps for communities built upon small numbers of discrete resources. Niches are not fixed and species can be added to a community by reducing average niche breadth in response to invasion. Unlike individuals, populations are compressible. Although extinction rates within a community would increase, this would be an expected response to an increasing rate of species production, or prolonged diversification, within a region. This relationship seems obvious to us now, but was not part of the mainstream of community ecological thought for decades.

The second idea that has hindered community ecology is that local processes come to equilibrium rapidly compared with evolutionary processes involved in species production and the extension and contraction of geographical distribution. Species production occurs at intervals of 10^5 years or more (Magallón & Sanderson 2001; Ricklefs 2003b) whereas competitive exclusion in model systems and microcosms takes 10^2 generations or fewer. How can we narrow this gap?

To answer this question, we should begin by asking whether the differences ecologists have perceived for the past 40 years are, in fact, real. I believe we have misled ourselves by allowing models and microcosm experiments, which concern systems with discrete boundaries and simplified structure, to inform us about natural systems. Certainly competition, predation and other interactions between populations occur in nature (Paine 1974; Connell 1983; Schoener 1983; Wellborn *et al.* 1996), and models and microcosms have helped us to understand the dynamics and outcomes of these processes (Morin 1999). However, the existence of these processes, including their expression in the organization of ecological communities, is not sufficient to confirm their role in regulating community diversity. Moreover, the time scales over which these interactions play out is longer in natural systems, by orders of magnitude, than in model systems and microcosms.

In nature, populations interact over vast areas – literally whole regions – with varied environments to which species are differentially adapted and within which their populations are regulated by powerful, density-dependent restraints (Chesson 2000).

The population of any particular species may be distributed over large areas encompassing a variety of environments. Populations also vary in the degree of their geographical and ecological range (Brown 1984; Gaston 1998, 2003). Regardless of their extent, populations are given coherence by movements of individuals within them. Ecologists have recognized this property of movement when they developed metapopulation theory and landscape ecology, including source-sink population dynamics. Thus, no one part of a population has dynamic properties that are independent of another part, although the degree of connection may diminish with distance or with barriers to dispersal.

As movements of individuals give populations coherence within regions, interactions between populations also play themselves out over entire regions. Thus, as emphasized by many ecologists (Pimm & Rosenzweig 1981; Rosenzweig 1981, 1991; Shmida & Ellner 1984; Kotler & Brown 1988) spatial variation in environmental conditions becomes a critical dimension of the niche space that competitors partition through evolved specialization and population interactions (Brown 1984; Holt 1987; Holt & Gaines 1992). Nevertheless, identifying axes of niche partitioning in some communities, such as the trees of tropical forests, poses a difficult problem. Although many studies have shown partitioning based on slight variations in elevation and soils (Tuomisto & Ruokolainen 1994; Tuomisto *et al.* 1995; Clark *et al.* 1999; Valladares *et al.* 2000), local determinists are still faced with the coexistence of 100 or more species of tree within small, apparently homogeneous areas where every other individual is a different species. This has led to a number of proposals for local coexistence based on differences in regeneration niches (Grubb 1977; Ricklefs 1977; Denslow 1987), dispersal limitation (Dalling *et al.* 1998; Hubbell *et al.* 1999; Wright 2002), and strong intraspecific density dependence caused by species-specific pathogens (Janzen 1970; Connell 1978; Clark & Clark 1984; Huntly 1991).

The conundrum of local determinism also stimulated Hubbell (2001) to explore the possibility that species of tropical trees (and other organisms) are ecologically and competitively equivalent and thus that coexistence is not constrained by competition. Hubbell's model is a quintessentially historical theory in that diversity represents a balance between speciation and extinction, and the steady-state species number within a region is a product of the size of the region (number of individuals) and the rate of speciation, both of which are regional/historical rather than

local/ecological factors. Hubbell's is a theory of rate and area, along the lines of J. C. Willis's (1922) 'age and area,' even to the point of using a mutation model of species production. In addition, because diversity within Hubbell's metacommunity reflects a random sampling process, there is a direct correspondence between local and regional diversity. It is clear, however, that species are not ecologically equivalent and that Hubbell's model will require modification to stand as a general hypothesis for diversity (Pitman *et al.* 2001; Ricklefs 2003a).

Realistic models of the regulation of diversity must incorporate specialization and environment-specific variation in competitive ability among species. One consequence of competition and other interactions within an entire region is habitat specialization (Brown 1984; Pulliam 2000; Morris 2003). The habitat distribution of each population is adjusted until the productivity of the population in favoured habitats balances the loss of individuals from less favourable habitats (Fretwell & Lucas 1970). All populations become adjusted in this way by range expansion and contraction until they have achieved stable population size and are demographically equivalent, if not ecological equivalent, within the region (Morris 1988). Populations are thus regulated by competition in a stable, size-dependent fashion within the region as a whole based on density-dependent regulation adjusted locally by the movement of individuals between localities, that is, from sources to sinks (Pulliam 1988).

Two aspects of geographical distributions are instructive: their uniqueness and the variation in their extent (Gaston 1998). The specialization of populations with respect to spatial variation in the environment is seen in the unique geographical and habitat distributions of species. These distributions are circumscribed by local factors, such as soil conditions, and by regional factors, such as geographical variation in temperature, precipitation and seasonality. The fact that species distributions rarely coincide emphasizes the subtle differences in the responses of populations to environmental factors within a region. Variation in the sizes of geographical ranges represents, to some extent, the adjustment of individual populations to competitive pressures within a region (see discussion by Holt 2003). The interaction between competition and distribution is seen most readily in the phenomenon of habitat expansion (generally, ecological release) on islands with reduced numbers of species (e.g. MacArthur *et al.* 1966; Cox & Ricklefs 1977; Ricklefs & Cox 1978; Ricklefs 2000). The influence of population processes on habitat distribution can also be seen in the positive relationship between breadth of habitat occupation and population density (e.g. O'Connor 1982; Gersani *et al.* 1998), driven by territorial behaviour or other manifestations of competition within populations (Fretwell & Lucas 1970). Within the same region, variation

in the extent of populations and their densities signals different competitive success, possibly related to differences in their evolutionary relationships with resource populations or with pathogens (Hochberg & Van Baalen 1998; Hochberg & Ives 1999).

Most of the variation in geographical and ecological extent of populations resides at a low taxonomic level, that is, between species within the same genus (Gaston 1998; Webb & Gaston 2000). Therefore, most of this variation is not related to phylogenetically conservative adaptations to habitat or climate (cf. Root 1988; Kukul *et al.* 1991), but rather would seem to reflect particular relationships of species to their biological environments, possibly to rapidly evolving pathogens. Although there is little evidence for or against this, one can imagine that the balance of host–pathogen adaptations influences the overall productivity of a host population and determines the degree to which the population can sustain itself in marginal environments (Hochberg & Van Baalen 1998). Thus, variation in ecological and geographical extent would reflect adjustment to both the competitive and the consumer–resource environments within a region. Consumer–resource interactions within a region may also be regulated in a frequency-dependent manner inasmuch as pathogens and predators might be selected to avoid rare prey or hosts in favour of more widespread populations. Thus, with respect to predators and pathogens, rarity might convey an advantage that reduces the probability of being driven to extinction by these interactions (Pimentel 1968; Ricklefs & Cox 1972; Rosenzweig 1973).

With competition leading to stably regulated populations within a region, the course of competitive exclusion, to the extent that it occurs, is plausibly extended to the time scale of species production. Accordingly, the rate of species production within a region directly influences the number of species within the region. Regional diversity and local diversity are connected through adjustments of the geographical and ecological extent of populations. As more species are added to a region and the intensity of competition increases, the average distributional extent of species decreases, leading to an increase in beta diversity. As population interactions do not directly constrain the number of species whose distributions include a particular point in space, alpha diversity also rises with an increase in regional diversity and average local population density declines. Thus, local (alpha) and beta diversity become spatially referenced sampling properties of the overlapping distributions of species populations within a region, leading to a direct connection between local and regional diversity.

Within the region as a whole, extinction must eventually balance species production, although there is no reason to presume that diversity has achieved a steady-state at a particular time and that the number of species within a

region is not either increasing or decreasing (Raup 1972; Knoll 1986; Ricklefs & Bermingham 2001). Extinction might be diversity-dependent because higher regional species richness leads to a restriction of average geographical range and population size, possibly increasing vulnerability to extinction. But what factors actually cause species to disappear from a region? The historical record revealed by fossils indicates that catastrophic environmental change, such as the impact event at the end of the Cretaceous period, or more gradual global environmental change, such as climate cooling at high latitudes during the late Tertiary, the diversification of new lineages of competitors or predators (Simpson 1953; Vermeij 1987), or biotic invasions (Vermeij 1991), can dramatically reduce the diversity of a region through extinction. Such extinctions may be highly selective, affecting some types of organisms more than others as the distribution of environment types shifts within a region (Jablonski 1989, 1991; Johnson *et al.* 1995; Cardillo & Bromham 2001; Svenning 2003).

More persistent background levels of extinction, which may or may not contribute importantly to the regulation of diversity, may be driven by imbalances in coevolved interactions between species. This is indicated by the observation that most variation in the extent of species ranges and the size of populations resides at a low taxonomic level and probably reflects special interactions between populations (Gaston 1998). As diversity within a region increases, average population extent decreases, the potential number of interactions with other populations increases, and the ability of a population to respond to these interactions by appropriate evolutionary adaptation might also weaken.

Species production is influenced by the characteristics of a region. The association of high species richness with tectonically active areas (e.g. Barthlott *et al.* 1996; Rahbek & Graves 2001) or regions with complex geography and physiography (Qian & Ricklefs 2000) is not accidental. Temporal variation over long periods, which divides and reconnects populations and drives evolutionary change, must also accelerate species production. Changes in landforms and climates within a region alter the array and configuration of habitats and shift interactions between populations. Thus, the balance between species production and extinction within a region probably changes continuously and species richness probably rarely approaches a steady-state.

This regional perspective provides a balance between the influences of species production and species interactions within regions and establishes a simple link between regional and local diversity. The regional perspective also can account for differences in species richness between regions. What remains for us to explain is the relationship between species richness and characteristics of the environment – the

many patterns of species diversity over ecological gradients. These patterns plausibly have both contemporary-ecological and historical-evolutionary origins, which are not mutually exclusive. Environments differ in their ability to support populations; they also have different extents and histories that shape the evolutionary diversification of the clades of organisms that fill them in. If we accept a role for evolution in producing the diversity–environment relationship, then we must find ways of partitioning the relative contributions of direct environmental influence and history in forging these patterns. Comparisons between similar environments in different regions address a different type of regional factor, namely variation in speciation and extinction caused by differences in physiography and history.

The evolutionary component of the diversity–environment relationship can be addressed, in part, by phylogenetic analysis of the relative ages of clades that have diversified within a particular ecological zone and those of clades originating from lineages that occur in other ecological zones. For example, the passerine bird fauna of South America, which is largely tropical and subtropical, includes about twice the number of species as that of North America, which is mostly temperate and boreal. A phylogenetic assessment of each of these avifaunas based on Sibley & Ahlquist's (1990) avian phylogeny constructed from DNA hybridization shows that the South American passerine fauna consists mostly of a large endemic radiation of flycatchers, antbirds, ovenbirds and their allies, supplemented by more recent clades, derived primarily from North America, that have, in some cases, diversified extensively in South America. The North American passerine fauna itself consists mostly of young clades that have diversified at a lower average rate than related lineages in South America (Ricklefs 2004b). Thus, the North American passerine fauna is relatively young – older, more tropical elements possibly disappeared with climate cooling in the late Tertiary – and diversification has not proceeded as rapidly as it has in South America. The relative rates of speciation and extinction can be estimated from the time intervals between branch points in a phylogenetic tree (Magallón & Sanderson 2001; Ricklefs 2003b), and thus some resolution of the balance between these processes in creating diversity gradients will be possible. It will be more difficult to determine whether time and rate of diversification determine patterns of diversity with respect to environment, or whether these historical components of diversity are constrained by local, ecological relationships.

THE RELATIONSHIP BETWEEN DIVERSITY AND ENVIRONMENT

Variation in diversity over ecological gradients continues to pose a problem. Correlations are often strong, but their

meaning is unclear. The patterns could be related to the capacity of environments to support coexisting species or they could be related to the ecological origins and evolutionary diversification of clades, that is, matters of time and space. The two cannot be readily distinguished, nor are they incompatible. Ecologically limited membership in local communities would, in any event, be filled out by evolutionary diversification and thus reveal the imprint of history. Phylogenetic analysis of the development of regional biotas can be used to trace the history of contemporary patterns of diversity, including ecological diversification. Evidence that less species-rich biotas are younger than more species-rich biotas might imply that diversity increases with age and that contemporary biotas are not in equilibrium. Such a finding would argue against local determinism of community membership. Comparisons of the evolutionary origins of forest trees suggest that temperate clades are mostly nested within tropical clades, indicating a generally younger age (Judd *et al.* 1994; Ricklefs 2004a).

It is also clear, however, that extinction can have a profound effect on diversity (Jablonski 1991; Latham & Ricklefs 1993a; Foote 2000; Svenning 2003). The phylogenetic consequences of large-scale extinctions (Heard & Mooers 2002), such as the late-Tertiary loss of European tree species diversity, have not been determined and they will depend on the degree to which extinction was selective (Latham & Ricklefs 1993a; Svenning 2003). Additional information concerning the history of a biota can be obtained from lineage-through-time plots (Nee *et al.* 1992, 1996). When the rate of diversification is constant, the logarithm of the number of lineages increases linearly as a function of time. If the production of new species within a region becomes more difficult as diversity increases, the apparent exponential increase in lineages through time should level off. In the case of the South American passerine avifauna, the exponential slope of the lineage through time plot remains constant (Ricklefs 2004b). In contrast, in the less diverse continent of Australia, the slope of the lineage-through-time plot falls off towards the present. Whether this is because of a filling of ecological space within the continent, or because of changing climate conditions, particularly the drying out of Australia during the late Tertiary (Kemp 1978; Cristophel & Greenwood 1989) cannot be distinguished.

Some patterns of species richness across barriers to evolutionary diversification can be explored through the distribution of habitat on phylogenetic trees (Webb *et al.* 2002; Ackerly 2003). For example, the frequency of transitions and the rate of diversification on either side of such barriers, such as freezing conditions of temperate environments or the saline and anoxic conditions of mangrove environments would provide evidence of the

historical development of patterns of species richness across such barriers. Distinguishing the degree to which ecological interactions constrain the rate of transition and diversification would require evidence of decrease in these rates over time, independent of ecological changes. It may be difficult to identify environments that have enjoyed long-term ecological stability, but the mangrove environment, which is buffered by marine conditions, may be one of these.

CONCLUSIONS

As shown here, patterns of diversity can be properly interpreted only within the broad context of regional and historical influences. I am also persuaded that the regional processes that contribute to large-scale patterns of diversity are the legitimate concerns of ecologists. Although particular patterns may reflect unique historical and regional circumstances, the processes through which these circumstances are expressed are amenable to comparative and experimental investigation, including genetic studies of population structure and incipient speciation. Diversity patterns should be a focus for integrating organismal ecology, including adaptation, population biology and evolutionary diversification. This new research programme has been developing for many years and is presently being accelerated by new molecular tools for investigating population structure and evolutionary adaptation, and statistical and analytical tools to describe evolutionary diversification and regional distributions. The following suggestions might help to make ecologists more aware of this research program and promote the further integration of ecology and evolution.

- 1 Ecologists should abandon circumscribed concepts of local communities. Except in cases of highly discrete resources or environments with sharp ecological boundaries, local communities do not exist. What ecologists have called communities in the past should be thought of as point estimates of overlapping regional species distributions. The extents of these distributions can be understood only by considering interactions within the region as a whole.
- 2 Ecologists should raise regional and historical factors to equal footing with local determinism in their influence on the diversity–environment relationship and geographical patterns of diversity in general. No precedents exist that should compel ecologists to prefer one or the other type of explanation.
- 3 Ecologists should assemble data that match the scale of the processes they are studying (Whittaker 1999; Rahbek & Graves 2001). For large-scale patterns of species richness, these should be local (point) estimates of diversity taken in nested sets, up to the scale of the whole region, that can be analysed to assess the roles of turnover among habitats and with distance within regions, with good controls on environmental conditions (see, e.g. Cox & Ricklefs 1977; Cody 1993; Pitman *et al.* 1999).
- 4 Ecologists should quantify distributions of populations within regions with respect to space and environment (Gaston 2003), which can come from (3) above. Multidimensional descriptive statistics will be helpful towards this goal (Jongman *et al.* 1987; Legendre & Legendre 1998).
- 5 Ecologists should evaluate the underlying premise that dispersal integrates populations within regions, and they should explore incipient species formation within regions (Rosenzweig 1978; Rice 1987; Moritz *et al.* 2000). In both cases, molecular data can be used to estimate rates of gene flow within populations and the depth of genetic divergence between populations (Hartl & Clark 1997; Avise 2000).
- 6 Ecologists should assemble phylogenies of large clades to estimate rates of diversification of lineages and the relationship between speciation and extinction. The latter can be estimated from the net rate of diversification and the average time between splitting events inferred from contemporary populations (5, above: incipient species formation) (e.g. Magallón & Sanderson 2001; Ricklefs 2003b).
- 7 Ecologists should undertake phylogenetic analyses of diversification with respect to ecological zones, including rates of diversification within zones and adaptive shifts between zones, perhaps most useful for sharp stress barriers (frost, salt) (Farrell & Mitter 1994; Webb *et al.* 2002; Ackerly 2003; Cavender-Bares & Wilczek 2003; Reich *et al.* 2003).
- 8 Finally, ecologists should ask whether generalities can emerge from this research programme, or merely a set of unique cases for which one cannot distinguish the underlying processes controlling patterns of diversity. If diversity did, in fact, represent a balance between local interactions and regional production of species, it would be pointless to devise tests that would reject one or the other explanation. We may not be able to estimate the relative contributions of local and regional/historical processes at each spatial and temporal scale of a hierarchy of diversity patterns. It is more important, however, that this integrated perspective leads to new ways of thinking about the relationships among species and the development of diversity patterns, which in turn will promote research on various implications of the regional perspective that are amenable to direct measurement, such as the genetic structure of populations and the relationship

between point diversity, beta diversity, and regional diversity. Assembling such data for a wide range of species might then lead to generalizations about diversity patterns that are more solidly grounded in the processes that produce them.

ACKNOWLEDGEMENT

I am grateful to David Currie, Stephen Heard, Nicolas Gotelli, Susanne Renner and an anonymous reviewer for insightful comments on the manuscript.

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Editor, Nicholas Gotelli

Manuscript received 25 September 2003

First decision made 22 October 2003

Manuscript accepted 10 November 2003

Manuscript exceeded normal length