

Historical and ecological dimensions of global patterns in plant diversity

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Prior to the development of population and community ecology in the 1960's, global patterns of species diversity, particularly the increase in diversity towards the equator, were explained by the greater age and more stable environment of the tropics or by a combination of age and area. Ecologists later envisioned competitive and consumer-resource interactions among populations as regulating the number of species in local ecological communities. The expression of these interactions in patterns of species richness would require that ecological limits to local coexistence depend on the physical environment. Advocates of local and regional processes have been unable to reconcile their views, partly because of traditions in ecological research and partly because of problems of scale in time and space. Resolution of these issues will require (i) attention to the scale at which patterns in diversity are established, (ii) models of the way in which local and regional processes interact with the physical environment and geography to influence diversity, (iii) testable predictions arising from both viewpoints (*e.g.*, community convergence as a consequence of local determinism), (iv) historical reconstruction of regional and local biotas, and, ultimately, (v) a new concept of interactions between populations and their environments over a hierarchy of temporal and spatial dimensions from the local habitat to entire regions. Approaches to understanding patterns of diversity include comparisons of local and regional taxonomic richness, which typically show a close correspondence between the two, and comparisons of richness in areas of similar climate but different regional diversity, which often exhibit regional effects. Phylogenetic reconstructions and calibrated molecular clocks now provide a means to estimate ages and rates of diversification, both of which contribute to global patterns of diversity. Finally, interactions between populations take place over regions as well as within communities. On balance, regional comparisons of patterns of species richness suggest that large-scale processes (*i.e.*, species formation) and unique historical and geographic circumstances have had a strong impact on patterns of plant diversity. Moreover, the correlation between diversity and environment may reflect, perhaps to a large extent, the history of ecological diversification of plants from primarily wet tropical origins.

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Introduction: A history of ideas about diversity

Large-scale patterns of plant diversity have been known in general terms since early natural history explorations of the earth in the

18th and 19th centuries (Huston 1994; Rosenzweig 1995). The most conspicuous of these patterns is the decrease in species richness with increasing latitude, although diversity also follows strong trends in relation to primary pro-

ductivity and certain stress factors in the environment. Explanations for diversity patterns are of two kinds that often are distinguished as alternative rather than complementary. On one hand, regional processes responsible for the production of new species tend to increase diversity within large areas. On the other hand, local population processes, including competition and various interactions with predators, parasites, and pathogens, tend to limit membership within local ecological communities. A reasonable view is that diversity represents a balance between local and regional processes and that the relative dominance of one or the other depends on the scale at which diversity is considered (Rahbek & Graves 2001; Willis & Whittaker 2002).

Until the 1960's, explanations for diversity patterns focused almost exclusively on large-scale processes and were mostly historical in nature. For example, Alfred Russel Wallace (1878) attributed the greater diversity of the tropics to the greater age of tropical regions and their having escaped the catastrophic extinctions caused by glacial climates at higher latitudes.

“The equatorial zone, in short, exhibits to us the result of a comparatively continuous and unchecked development of organic forms; while in the temperate regions there have been a series of periodical checks and extinctions ... In the one, evolution has had a fair chance; in the other, it has had countless difficulties thrown in its way. The equatorial regions are then, as regards their past and present life history, a more ancient world than that represented by the temperate zones, ...”

John Willis (1922) believed that diversity was primarily related to species production, which he surmised would produce greater numbers of species in larger and older regions, hence the title of his book, *Age and Area*. As recently as 1960, A. G. Fischer postulated that rates of species production were higher in tropical

compared to temperate regions, a difference that could be attributed to the greater energy input and temperature of tropical systems, which hastened all biological processes (Rohde 1992). Additional regional-scale processes that contribute to patterns of diversity on a global scale include the mixing of regional biotas when barriers to dispersal are removed (*e.g.*, Vermeij 1991) and regional extinctions owing to catastrophic events or rapidly changing climates and landforms.

The eclipse of history

The emphasis in explanations for diversity patterns shifted away from regional and historical factors in the 1960's with the infusion of population approaches into ecology. The development of population models (Lotka 1925, 1932; Volterra 1926) and experiments with interactions between species in microcosms (Gause 1934) provided a foundation for interpreting the ecological distributions of organisms, particularly the concept of the niche (Hutchinson 1957, 1959; Vandermeer 1972; Prinzing *et al.* 2001), and the observation of ecological isolation, or resource partitioning, between species (Lack 1944, 1947). The competitive exclusion principle that no two species could coexist on the same limiting resource (Hardin 1960) was extended to entire communities of organisms to establish limits (limiting similarity) to the packing of species within ecological space, which ultimately limited the diversity of the local community (Elton 1927, 1946; MacArthur & Levins 1967; May 1975). Finally, ecologists could claim patterns of species richness as a problem amenable to population modeling and experimentation within the temporal and spatial scales of ecological thinking at the time (MacArthur 1972). The adoption of this powerful paradigm to explain diversity has been referred to as the “eclipse of history” (Kingsland 1985) because historical and regional explanations were largely set aside.

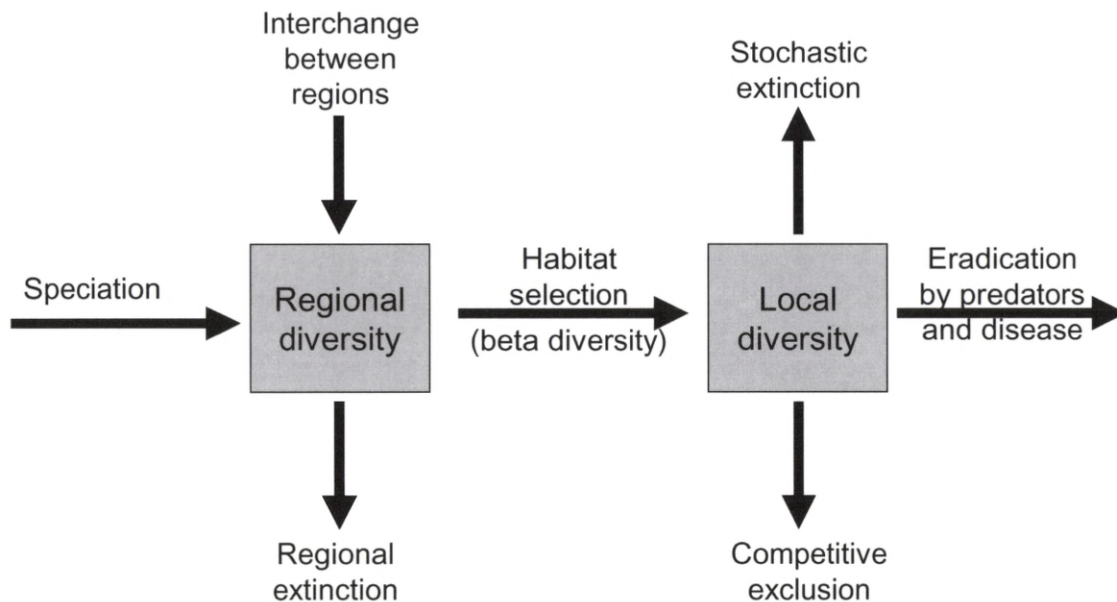


Fig. 1. The connection between regional and local diversity through the habitat breadth of individual species and the turnover of species between habitats (beta diversity) (after Ricklefs & Schluter, 1993).

Local, regional, and beta diversity

When membership in local communities is limited by species interactions, variation in diversity must result from differences between communities in the total niche space available or in the way species partition niche space through specialization and niche overlap (MacArthur 1965). Furthermore, these differences must be related to conditions of the physical environment if patterns of diversity are to become established. This could work through a number of mechanisms. For example, higher productivity could lead to greater habitat structure and complexity (Orians 1969; Connell 1978); less variable environments might allow more specialization and smaller population sizes (Connell & Orians 1964; Pianka 1966); physically benign environments might allow greater diversification of life styles, thereby providing the potential for creating more niche axes (Dobzhansky 1950; Terborgh 1973; Kleidon & Mooney 2000). The theory of stochastic popu-

lation changes would additionally suggest that larger populations are more resistant to extinction (Goodman 1987; Boyce 1992; Lande 1993), creating a connection between productivity and diversity (Currie 1991; Wright *et al.* 1993).

Even population biologists realized that the ultimate source of diversity must be species production, which generally takes place within large regions. Robert H. MacArthur (1965), one of the architects of the revolution in community ecology of the 1960's, recognized the importance of the region as the crucible of species production. However, he maintained that local diversity was independently limited by constraints on coexistence of populations of different species.

"If the patterns [of species diversity] were wholly fortuitous and due to accidents of history, their explanation would be a challenge to geologists but not to ecologists. The very regularity of some

of the patterns for large taxonomic groups suggests, however, that they have been laid down according to some fairly simple principles, ...”

“... if the areas being compared are not saturated with species, an historical answer involving rates of speciation and length of time available will be appropriate; if the areas are saturated with species, then the answer must be expressed in terms of the size of the niche space ... and the limiting similarity of coexisting species.”

Thus, MacArthur recognized both the connection between local and regional diversity and their independence. This connection is shown in a simple diagram in Fig. 1, where factors that influence regional and local diversity are indirectly connected through habitat specialization – the “beta” component of species diversity. Accordingly, where two regions differ in diversity but matched local habitats have the same diversity, the discrepancy is reconciled by differences in habitat specialization. Where local diversity within habitats is conserved, higher regional diversity must be accompanied by increased habitat specialization.

This principle was elaborated by Martin Cody (1975) who used Whittaker’s (1972) concept of beta diversity, that is, turnover of species along habitat gradients, to link ecologically constrained local diversity to historically differentiated regional diversity.

“These species-packing levels [local diversity] can be adequately explained by competition theory and by the constraint of a limiting similarity, between species on a resource gradient, that cannot be exceeded ... Thus patterns in α -diversity conform well with simple theoretical expectations that ignore history.”

“However, diversity differences, and in particular the marked differences in β -diversity between continents, must have explanations with a strong component of history and chance, both in the

production and distribution of various habitat types and in the buildup through time of their respective bird faunas.”

The broadening of community concepts

Although most ecologists would not dispute the influence of large-scale processes on regional diversity, fewer accept that these processes also leave their imprint on species richness within local communities. Certainly the ecological concept of the community has changed considerably since the 1960’s. Indeed, the strong stance over local determinism taken by some ecologists was rather ironic in view of trends in community ecology at the time. For example, although a Clementsian view of discrete community structure (Clements 1936) was largely abandoned by the 1950’s (Gleason 1926; Whittaker 1953; McIntosh 1967), the development of community theory in the 1960’s and 1970’s was largely based on a closed community concept (the “community matrix”) and lacked an evolutionary context (MacArthur & Levins 1967; May 1975; Morton *et al.* 1996). In addition, while R. H. MacArthur was rejecting regional and historical influences in favor of local constraints on community diversity, he also developed, with E. O. Wilson, the equilibrium theory of diversity on islands, which is driven by the “external” process of colonization (MacArthur & Wilson 1963, 1967). These inconsistencies illustrate the general schizophrenia of ecology at that time, torn as it was between its natural history background and the development of a rigorous theoretical and experimental program (Kingsland 1985; McIntosh 1985).

The 1980’s saw a broadening of the ecological concept of the community with the development of metapopulation models that emphasized the spatial structure of populations and movement of individuals between patches of suitable habitat (Hanski 1982, 1997), and source-sink relationships between

populations in habitats of high and low productivity (Pulliam 1988) leading to mass effects whereby the diversity of local communities is influenced by immigration of individuals from neighboring communities (Shmida & Wilson 1985; Stevens 1989). This theme of the distribution of populations among habitats has been developed theoretically by Robert Holt and others (Holt 1996, 2003). Thus, for many ecologists the community concept currently encompasses gradients of habitat conditions or mosaics of habitat patches within landscapes (Turner 1989). Still, evolutionary changes in populations and the production of new species are not a part of the community equation. Ecological systems, whether they are homoge-

neous habitats or more complex habitat mosaics, still come into equilibrium rapidly as a result of individual movements and population interactions. Ecological communities, by whatever definition, are seen as samples of the regional species pool filtered by ecological tolerances of individuals to local conditions and interactions among coexisting members of the ecological association (Zobel 1992, 1997; Weiher & Keddy 1999).

Testing hypotheses about diversity

Ideas about the establishment and regulation of diversity at any scale can be tested only when they make unique predictions. Demonstrating

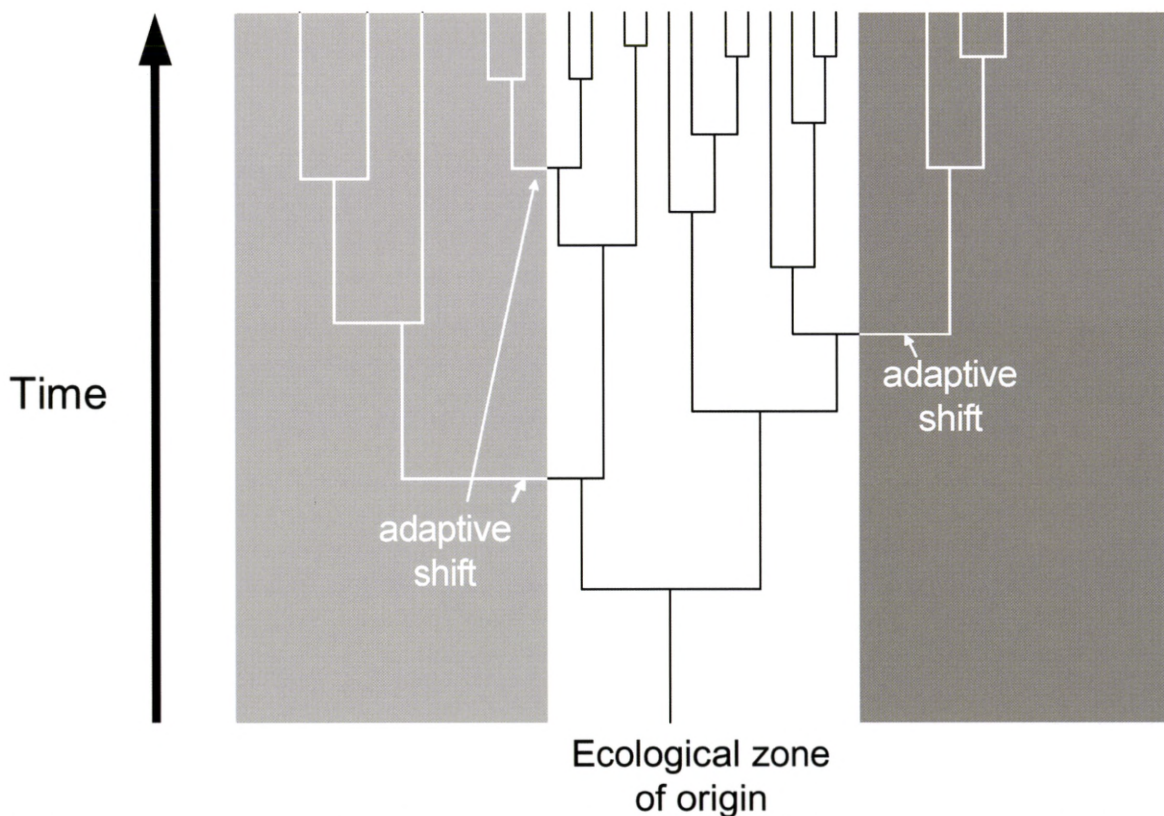


Fig. 2. An illustration of how the diversity of a clade can vary with respect to ecological conditions because of evolutionary constraints on adaptive transitions between different habitats or ecological zones. Adapted from Farrell and Mitter (Farrell & Mitter, 1993).

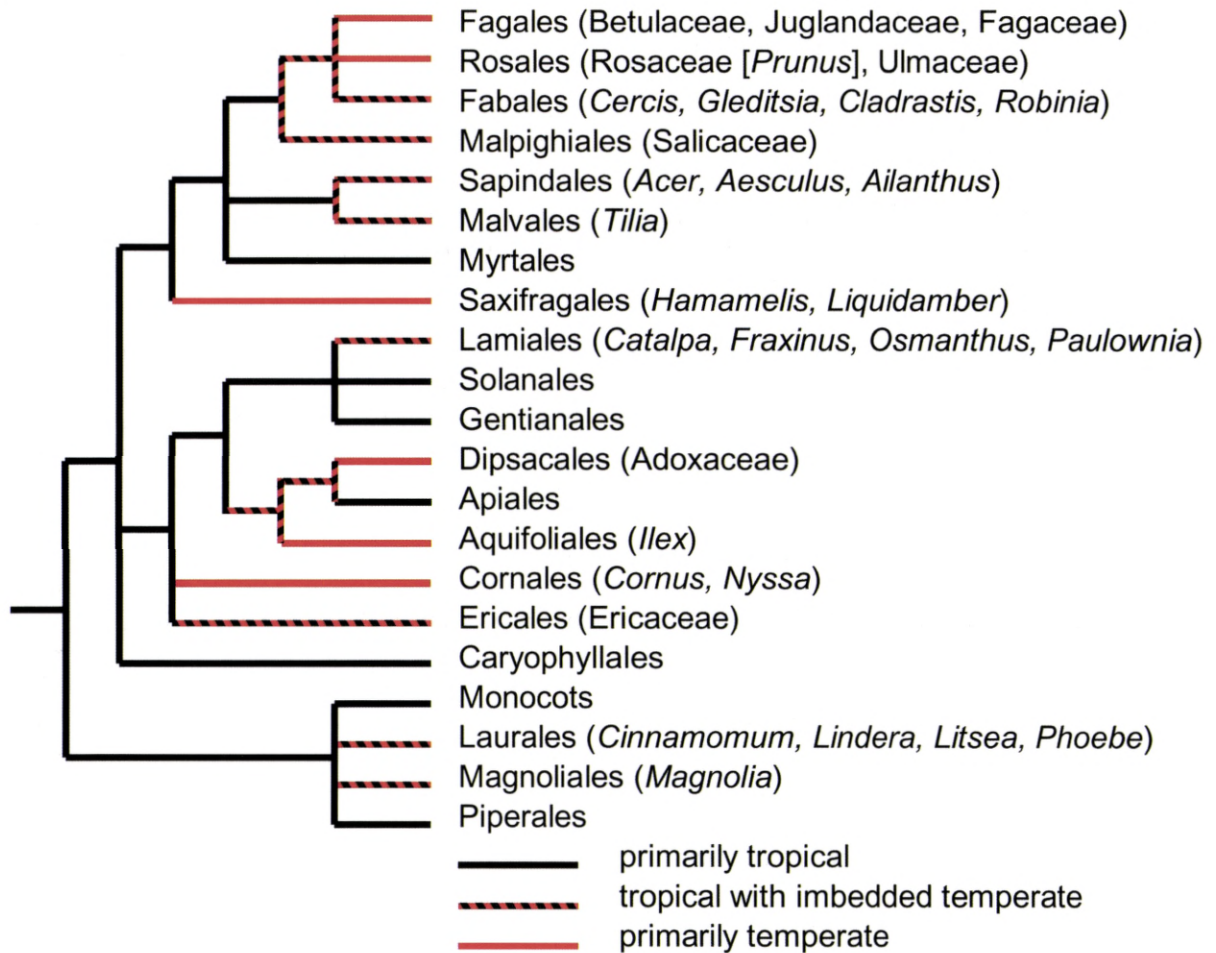


Fig. 3. Phylogenetic relationships among orders of angiosperm plants that comprise most of the tree floras of the New World. Prominent clades of temperate trees are indicated, along with the inferred region of each of the branches. The phylogenetic tree is based on Soltis *et al.* (2000).

the existence of competition and other interactions within communities, which was a major task of the 1970's and early 1980's (Pianka 1973; Schoener 1974; Brown 1981), is not sufficient reason to assign control over diversity to local factors (Connor & Simberloff 1979). Useful tests must address diversity directly, examining predictions about patterns in diversity in relation to local and regional factors. The strongest predictions arising from hypotheses about local ecological control over diversity are

(1) that species richness is correlated with physical conditions in the environment and (2) that local species richness is independent of variation in the size of the regional pool of species (the principle of convergence).

The correlation of diversity with the local environment

The first prediction has been addressed by many studies relating diversity to various aspects of the environment, often climate vari-

ables or indices of moisture or heat flux calculated from temperature and precipitation (*e.g.*, Currie 1991; O'Brien 1998; Kaspari *et al.* 2000; Whittaker & Field 2000; Francis & Currie 2003). Such relationships often account for a substantial portion of variation in species richness over many scales of analysis, although which environmental variables are the most important may vary with the dimension of the study (Rahbek & Graves 2001; Willis & Whittaker 2002). However, the diversity-environment correlation can also result from historical (evolutionary) factors, as diagrammed in Fig. 2.

Each lineage of organisms arises within a particular ecological zone to which it is adapted. With time, the lineage may diversify to form a clade within the ecological zone of origin, but over time some branches may make evolutionary transitions into different environments (Farrell *et al.* 1992; Latham & Ricklefs 1993b). Examples of such transitions would include the evolution of freezing tolerance and the invasion of temperate latitudes or the much less frequent evolution of tolerance to the high salt concentrations and anoxic sediments of mangrove environments. During the early Tertiary, when most families of modern plants initially diversified, the world was largely tropical, even at high latitudes (Wolfe 1975, 1978; Behrensmeyer *et al.* 1992). From this beginning, an evolutionary scenario could easily account for the latitudinal gradient of diversity between present-day tropical and temperate latitudes.

More than half the families of flowering plants (52%) are restricted to the tropics, and only 15% are distributed primarily in temperate latitudes (Ricklefs & Renner 1994). Most clades of exclusively temperate (frost tolerant) plants are relatively recent in origin and are imbedded in larger clades with predominately tropical distributions. This is indicated for lineages that constitute temperate forest trees in

Fig. 3. The most prominent, primarily temperate lineages of trees comprise the orders Fagales and Rosales, which are imbedded within the largely tropical rosid clade. However, each of the other orders within this clade, except for the Myrtales, has a few temperate arborescent representatives, for example, willows (*Salicaceae*) within the Malpighiales, maples (*Acer*) within the Sapindales, and linden (*Tilia*) within the Malvales. Thus, the transition from frost-sensitive to frost-tolerant has occurred many times among woody plants, but not often enough to build diversity in temperate tree floras to the levels found in the tropics. Adaptive barriers may restrict lineages to more stressful, less productive environments as well as to the tropics. Many clades found only in temperate areas have diversified there but have not reinvaded tropical areas (Judd *et al.* 1994), plausibly because their adaptations for tolerating freezing make them poor competitors in tropical environments. Some temperate clades, such as the oaks (*Fagaceae*), enter tropical latitudes, but only at high elevation.

Of course, taxonomic richness is a function of the rate of diversification of lineages as well as the number and age of lineages within an ecological zone (Cardillo 1999; Ricklefs, *in press*). As better phylogenetic hypotheses and time calibrations are developed for plants (*e.g.*, Renner *et al.* 2000; Renner & Meyer 2001), it will be possible to estimate the age and average rate of diversification (speciation minus extinction) within clades (Eriksson & Bremer 1992; Magallón & Sanderson 2001). Among passerine birds, for example, for which a broadly sampled phylogeny based on DNA hybridization is available (Sibley & Ahlquist 1990), the greater diversity of the South American avifauna compared to that of North America is due, in part, to a single old endemic clade of suboscine passerines (flycatchers and their relatives) represented by more than 900 species

(nearly a tenth of all birds!), and in part to the more rapid diversification of younger clades in South America compared to North America (Ricklefs, in press). Thus, the diversity discrepancy between North and South America is due to both the age and rate of diversification of the avifauna. Whether the rate difference is related to the extensive area of tropical environments in South America or to other features, such as the Andean orogeny (Fjelds  & Lovett 1997; Rahbek & Graves 2001), remains to be determined (*e.g.*, Chown & Gaston 2000; Buzas *et al.* 2002).

Regional diversity anomalies

The role of regional and historical factors in shaping patterns of regional diversity is well known for plants. One of the most striking examples comes from the deciduous forests of the North Temperate Zone. The climates of eastern North America, Europe, and eastern Asia are similar and their tree floras share many of the same genera. Yet Europe has fewer species of trees (ca. 150) than North America (ca. 250) and, especially, eastern Asia (ca. 750). Historically, these floras show quite a different pattern (Fig. 4). Focusing only on tree genera,

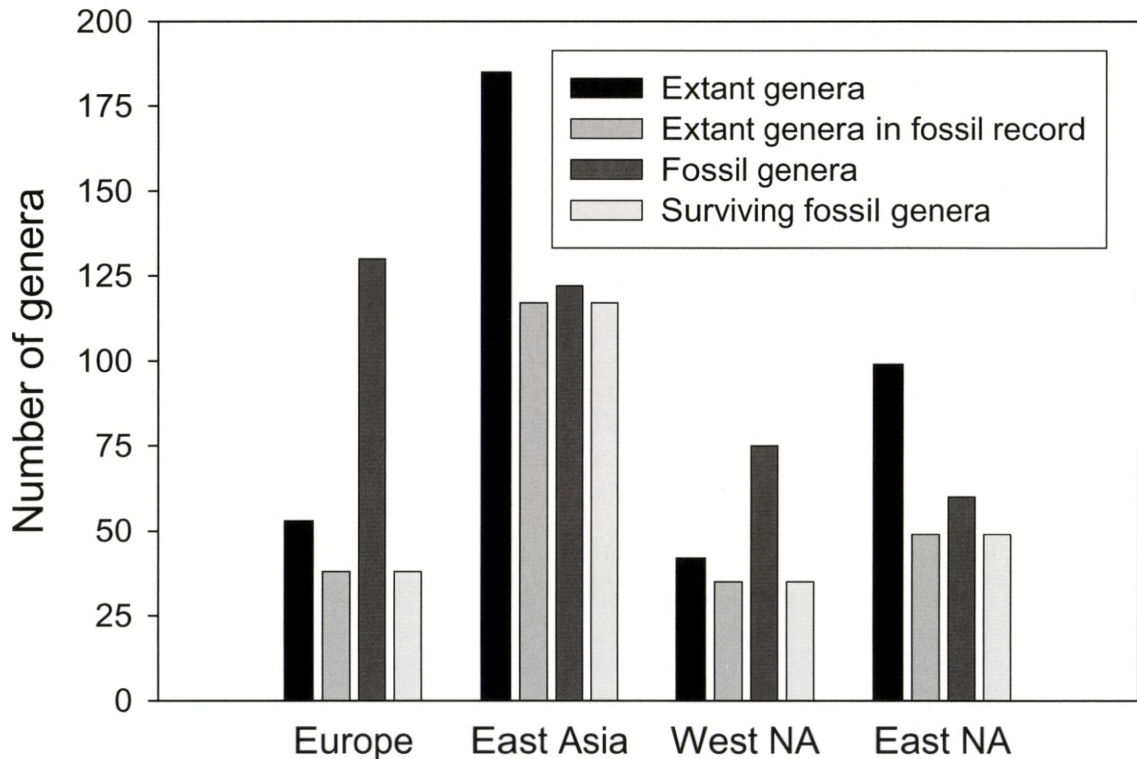


Fig. 4. Number of genera of extant and fossil trees in Europe, eastern Asia, and western and eastern North America. The proportion of the extant genera in Tertiary floras (second bar relative to the first) is a measure of the completeness of the fossil record, which is excellent for Europe and western North America. The proportion of fossil genera that survive (fourth bar relative to the third) provides an indication of extinction resulting from late-Tertiary and Pleistocene climate cooling. Extinction was pronounced in Europe and western North America but less so in eastern North America and, especially, eastern Asia. Data from Latham and Ricklefs (1993a).

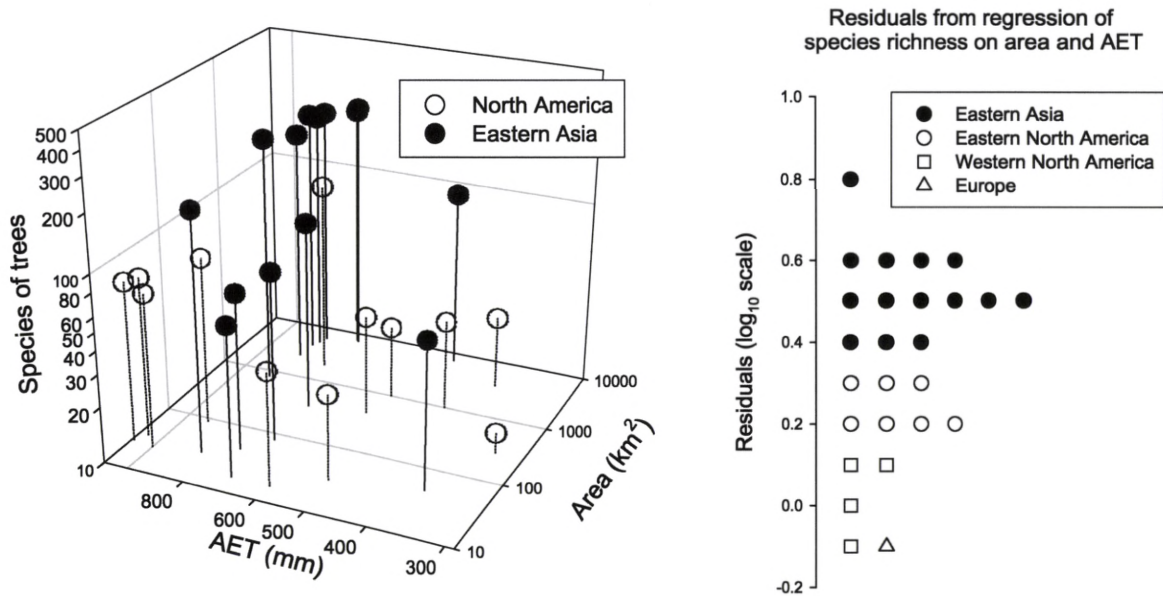


Fig. 5. An analysis of covariance (ANCOVA) relates the number of species in tree floras in moist temperate areas of eastern Asia and North America to flora area and actual evapotranspiration (AET), with a significant additional effect of region ($F_{3,20} = 34, P < 0.0001$). Residuals from the regression of species richness on area and AET are shown at right, and indicate that diversity in eastern Asia is 1.9 times greater than in eastern North America and 4.1 times greater than in western North America (ANCOVA model explains 94% of variance in species richness among floras). Unpublished analysis of data in Latham and Ricklefs (1993b, Table 1).

Table 1. Ages of the earliest fossils of mangrove genera with cosmopolitan distributions or restricted to the Indo-West Pacific (IWP) region. Most of the early Tertiary fossils are from the Tethys region of Europe while more recent first occurrences appear in the present-day IWP. From data compiled by Ellison *et al.* (1999).

Age	Cosmopolitan taxa	Old World endemics
Upper Cretaceous	<i>Nypa</i>	
Paleocene	<i>Rhizophora</i>	<i>Sonneratia</i>
Lower Eocene	<i>Avicennia</i>	<i>Bruguiera</i>
	<i>Pelliciera</i>	
	<i>Palaeo/Weatherellia</i>	
	<i>Acrostichum</i>	
Middle Eocene	<i>Lumnitzera/Laguncularia</i>	<i>Brownlowia</i>
		<i>Ceriops</i>
		<i>Kandelia</i>
		<i>Barringtonia</i>
Upper Eocene		
Oligocene		
Lower Miocene		<i>Camptostemon</i>
Middle Miocene		<i>Excoecaria</i>
		<i>Aegialitis</i>

which can be distinguished in the fossil record, it is apparent that the mid-Tertiary diversity of trees in Europe was much greater than at present and perhaps as high as that of eastern Asia. Species disappeared from Europe with late-Tertiary climate cooling and the onset of glacial climates (Sauer 1988), and most of the genera that were lost belonged to lineages with more tropical distributions, such as members of the Lauraceae (Latham & Ricklefs 1993a; Svenning 2003). Surprisingly, North America had lower tree generic richness during the mid Tertiary than either Europe or eastern Asia, suggesting a Eurasian origin for many clades of temperate trees combined with a failure to disperse to North America (Donoghue *et al.* 2001; Manos & Stanford 2001). However, fewer genera were lost in North America than in Europe as a result of climate cooling and glaciation, probably owing to the presence of adequate refuges in the southern part of the region (Elenga *et al.* 2000; Prentice & Jolly 2000; Williams *et al.* 2000; Yu *et al.* 2000).

Historical factors may also explain the extreme diversity anomaly in mangrove vegetation between the Indo-West Pacific (IWP) and the Atlantic-Caribbean-East Pacific (ACEP) regions (Chapman 1976; Saenger *et al.* 1983; Duke 1992, 1995; Ricklefs & Latham 1993; Morley 2000). The mangrove flora of the ACEP consists of 7 species in 4 genera that are pantropical in distribution, either at present or in the Tertiary fossil record. In contrast, the IWP region harbors at least 40 species in 17 genera; 14 of the genera are endemic to the region. Neither area nor local environment can explain the regional anomaly, which translates to a 2- to 3-fold difference in local (i.e., hectare scale) diversity (Chapman 1976). It is likely that mangrove lineages arising from terrestrial progenitors during the early Tertiary did so in the Tethys region of what is now Europe and spread both eastward into the IWP and westward into the ACEP regions (Ellison *et*

al. 1999). At that time, the known mangrove flora was pantropical, at least at the genus level. However, from the Eocene on, most appearances of new genera in the mangrove fossil record refer to IWP endemics and come increasingly from the IWP region itself. This suggests that the IWP has been the primary cradle of new mangrove lineages for the past 20-30 million years. No early first appearances of mangroves are known from the ACEP region and extant lineages have not diversified within the region. The difference may be related to the IWP region's extensive areas of shallow continental shelf with numerous islands in close proximity to extremely wet terrestrial environments, which are largely lacking from the ACEP region. Thus, diversity in this case would be related to geographical and historical factors affecting the evolutionary transition from terrestrial to mangrove environments, and diversification within the mangrove environment, rather than the conditions of the local mangrove environments. Time is also a factor, as diversification within the 15 clades of mangroves increases significantly with age as judged by taxonomic differentiation from terrestrial sister taxa (Ricklefs & Latham 1993).

Diversity anomalies that can be related to regional and historical factors emphasize the importance of large-scale influences in understanding patterns of diversity. In most cases, regional effects are not as great as the differences illustrated above for temperate trees and mangroves. Moreover, some "region" effects may be caused by general differences in the local environments between continents. For example, Morton (1993) has argued that differences in the diversity of several groups of animals in Australian deserts compared to other arid environments reflects the unique history of Australia, but primarily through the effect of history on local environmental conditions that include nutrient-depleted soils and

highly variable rainfall (see also Pianka 1986).

Considering the potential confounding effect of region and environment, it is important to separate the two statistically. An initial attempt at this uses an analysis of covariance (ANCOVA) in which differences in diversity between regions is tested with the influence of variation in environmental conditions controlled statistically. The approach is applied to the tree species richness of local floras in eastern Asia and eastern North America in Fig. 5 (Latham & Ricklefs 1993a). In this example, both flora area and actual evapotranspiration (a synthetic variable derived from temperature and precipitation and closely related to primary productivity) influence species richness, together accounting for 94% of the variance. However, when these factors are accounted for, floras in eastern Asia have on average almost twice as many species of trees as floras of similar size and climate in North America. By way of caveats, unmeasured variables, such as local topographic heterogeneity, might underlie the region effect, and statistical inference is clouded by non-independence of the diversity of floras within a region. Nonetheless, Qian and Ricklefs (2000) emphasized the importance of the geographic heterogeneity of eastern Asia, comparatively small areas of Pleistocene glaciation (Yu *et al.* 2000), and the broad connections between temperate and tropical forests as regional and historical factors responsible for the eastern Asia-eastern North America diversity anomaly.

Differences in diversity can be placed in a phylogenetic framework when the biotas of different regions share a common evolutionary ancestry. The temperate floras of eastern Asia (EAS) and eastern North America (ENA) are ideally suited for such comparisons because of the large number of shared genera of plants, including many disjunct genera that are found nowhere else (Li 1952; Hsü 1983; White 1983). If the representatives of a genus in Asia and

North America have a sister relationship, then one can assume that the lineages have the same age and initially exhibited generally similar ecological relationships. Accordingly, differences in diversity can then be related to different rates of diversification (Farrell & Mitter 1993). In the case of the EAS-ENA disjuncts, most of these genera have greater species richness in eastern Asia (Qian & Ricklefs 2000). Exceptions are found only in ENA genera whose distributions extend to the western part of the continent, where topographic and climate heterogeneity promote diversification. This comparison again underscores the importance of unique historical and geographical attributes of regions.

The relationship between local and regional diversity

Although regional and historical effects have a demonstrated influence on regional diversity, it is less clear that this influence extends down to the level of the local community. This seems to be the case for mangrove floras, as we have seen, and local forest plots in Japan harbor more species of trees than plots in similar environments in North America (Latham & Ricklefs 1993b). Another approach to the connection between local and regional diversity is to plot local diversity as a function of regional diversity for sampling areas having similar conditions but occurring in different regions. Terborgh and Faaborg (1980) used this approach with respect to bird diversity in selected habitats on islands in the West Indies. They found that local (within habitat) diversity increased with regional (island) diversity up to a point and then leveled off, which they interpreted as evidence for local limitation of community membership by interactions between species. Similar studies by Cox and Ricklefs (1977) and Wunderle (1985), employing censuses of birds within nine matched habitats on islands and nearby continental locations within the

Caribbean Basin, showed that local diversity increased as approximately the square root of regional (island) diversity, with beta diversity making up the remaining discrepancy between the two (Ricklefs 2000). Cornell (1985) used a similar approach for examining the diversity of gall wasps on oaks in California, in which case oak species were considered as regions and localities within a species' range were considered as communities. Many studies have followed upon these, and they generally support a connection between local and regional diversity (Cornell 1999), although Srivastava (1999) has cautioned against many pitfalls in this technique, including definitions of region and independence of samples.

That local diversity is sensitive to regional diversity has been shown in several empirical analyses, but the foundation for this conclusion is weakened by a number of considerations. The first is the quality of the data. Few diversity surveys have been conducted with the explicit purpose of testing the local-regional relationship (Caley & Schluter 1997), and these analyses have mostly relied on data gathered for other purposes and lacking a statistically efficient sampling structure. An exception to this is the survey of local species richness of birds in carefully matched habitats in the Caribbean Basin, which shows particularly well an increase in both local diversity and turnover of species over a habitat gradient in response to increasing regional diversity (Ricklefs 2000).

The second problem is the definition of 'local' and 'regional', which are necessarily arbitrary points along a continuous scale. In fact, however, the important aspect of the comparison is that the two are sufficiently separated that the local scale neither approaches the regional scale closely enough to generate a correlation between the two nor is so small as to result in insensitivity owing to inadequate sampling (Loreau 2000). More important is

the difficulty of obtaining statistically independent samples of the relationship between local and regional diversity. Because life arose once on earth, no region is strictly independent, and the lack of independence increases as comparisons between 'regions' are restricted to progressively smaller areas. Ideally, one would limit sampling to one local plot per continent (Schluter & Ricklefs 1993; Caley & Schluter 1997), but this would be self-defeating and would additionally pose the problem of defining 'region' for a particular locality.

The so-called regional species pool is usually considered as the set of species that potentially could occur in a particular local environment, taking into account the geographic distribution, habitat distribution, and dispersal abilities of species within a region. Membership in a local community is then restricted primarily by interactions between species. A broader concept of region allows for evolutionary shift of habitat and geographic range and thus increases the potential membership in a local community but extends the time scale over which local diversity is allowed to develop. As pointed out below, this problem of scale has been a major sticking point in understanding the continuity between local and regional processes.

A third problem related to the local-regional relationship is the direction of causation. A significant correlation between diversity at local and regional scales could arise from the diversity-generating influence of regional processes. However, one could reasonably entertain the idea that regional diversity merely sums ecologically constrained local diversity over a large area. Distinguishing these hypotheses hinges on beta diversity – the turnover of species between habitats. Control of diversity solely by local interactions makes no prediction about the relationship between beta diversity and local diversity. Conversely, when diversity is balanced between regional and local factors, local

and beta diversity should vary in direct relation to each other, as shown in the few cases in which both have been measured over defined habitat gradients.

Reconciling the time scales of local and regional processes

The major difficulty for ecologists who wish to integrate local and regional processes is the problem of temporal and spatial scale. We have been brought up on a long tradition of theoretical and experimental population biology, which has taught us that ecological processes attain steady states within a few tens of generations – far too quickly for local ecological systems to bear the imprint of processes playing out over longer time scales (Ricklefs 1989). Yet many data indicate that local and regional systems are directly connected on a continuum. Reconciling the problem of scale has two solutions. The first of these arises from Steve Hubbell's (2001) concept of zero-sum ecological drift, which eliminates the possibility of exclusion from a community by competitive disadvantage, thereby reducing local processes to random factors whose time course is proportional to the number of individuals in the system. The second arises from the achievement of demographic equivalence within regions through adjustment of habitat distribution and within-habitat niche breadth.

Hubbell's zero-sum ecological drift model

Hubbell's insight is grounded in the amazing diversity of tropical trees: up to 300 species per hectare, practically a different species encountered with every other individual in a local forest plot. Hubbell sees little opportunity for habitat partitioning and considers the possibility that species are ecologically equivalent. He then explores the implications of this idea through a zero-sum model in which each individual death is replaced by one individual that

is the offspring of a randomly selected tree. New species arise through a random process of speciation, which can range from a mutation-like event arising from a single individual to the partitioning of the population of a single species into mother and daughter species. According to this theory, and using the mutation model of speciation, diversity is determined only by the number of individuals in the so-called metacommunity (J_M) and the rate of speciation (v), such that $S \approx -2J_M v \ln(2v)$. Extinction is stochastic. Thus, in Hubbell's model, diversity in a metacommunity of a given size is determined strictly by the rate of a large-scale process – speciation – and diversity within small areas is a random sample of the total diversity of the metacommunity. Hence, there is a perfect relationship between local and regional (metacommunity) diversity and no limit to membership in a local 'community' other than the number of individuals.

Appealing as Hubbell's model may be, it does not apply well to real systems. First, although appropriate data are hard to come by, the model predicts a particular distribution of ages for splitting events (speciation) in the phylogenies of clades that make up the metacommunity. In this respect, theory and observation do not appear to match closely (Ricklefs 2003a). In particular, the fission model of speciation produces new species with long expected times to extinction and the metacommunity reaches a steady state level of diversity well above observed values. The problem with Hubbell's model is that it predicts too much diversity. Furthermore, differences in steady state diversity within metacommunities of similar size must be matched by equivalent differences in the rate of speciation. It is difficult to conceive of a ten-fold difference in the rate of speciation of forest trees between Amazonia and temperate eastern North America, although phylogenetic reconstructions will soon provide the information on intervals

between speciation events needed to test this idea (Ricklefs 2003b).

Second, Hubbell's model presupposes that species do not differ ecologically so as to have refuges from competitive exclusion. There is no frequency or density dependence in the model. Such ecological equivalency is contradicted by virtually all studies of habitat and microhabitat distribution in tropical plants to a degree that considerably weakens the premise of ecological drift (Ashton 1969; Tuomisto & Ruokolainen 1994; Tuomisto *et al.* 1995; Clark *et al.* 1999; Svenning 1999, 2001; Wright 2002). Thus, we are faced with the difficulty of balanc-

ing two opposing points of view, one of which sees numerous species of trees growing side by side under the same ecological conditions, the other of which sees turnover of species along habitat gradients, including fine distinctions among soils within the same local area. One might argue that the tropics are subdivided into many metacommunities defined by edaphic and climatic conditions, and a community drift process determines diversity within each of these. However, there is a much simpler way to resolve this issue that fully integrates both points of view.

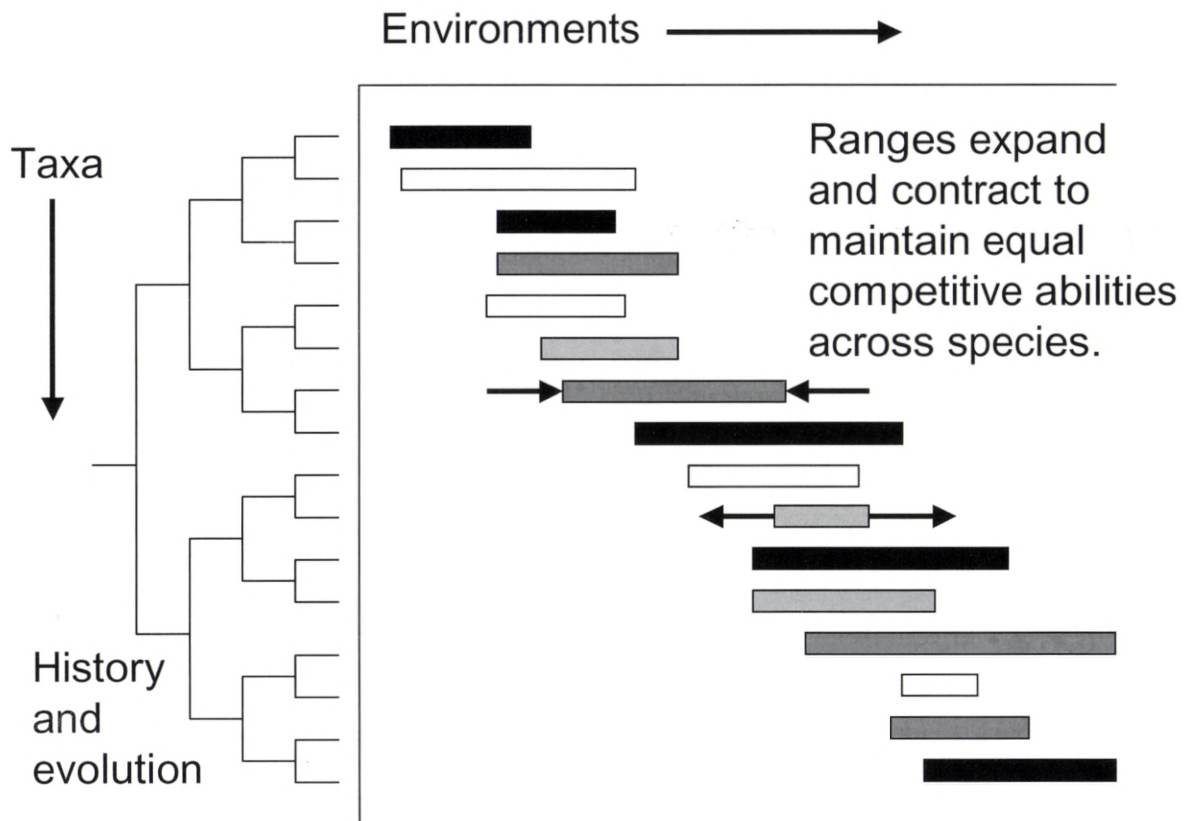


Fig. 6. A diagram of the evolutionarily and ecologically dynamic distribution of species over environmental gradients within a region. Distributions of species are maintained stably by density-dependent competitive interactions, but may undergo expansion or contraction following changes in the environment or evolutionary changes in traits affecting species interactions.

Table 2. Variance apportionment among taxonomic levels for the log-transformed abundance of trees on the BCI forest dynamics plot averaged over censuses made in 1982, 1985, and 1990. Data from the Center for Tropical Forest Science website (<http://www.ctfs.si.edu/data/data/data.htm/>); taxonomy according to the Angiosperm Phylogeny Group website (<http://www.mobot.org/MOBOT/Research/APweb/welcome.html>).

Source of variance	Sample	Percent of variance in population size	
		Observed data	Randomized data
Orders within angiosperms	22	7	1
Families within orders	32	0	0
Genera within families	130	22	0
Species within genera	124	71	99

The integration of local and regional processes

The idea is this. Species production within regions and population interactions having demographic consequences within local communities are well-established processes in ecology and evolutionary biology. However, because individuals move across the landscape more rapidly than population interactions come into a steady state locally, interactions between species occur within regional landscapes rather than being limited to local areas. The outcome of changes in these interactions caused by environmental change or by evolution within one or more populations is more frequently an expansion or contraction of ecological and geographic breadth, than the exclusion of a species from a region. These adjustments of distribution result in the equalization of average regional population growth rates close to zero, similar to the manner in which Hubbell (2001) imagined that life-history trade-offs might equalize population growth rates locally. Thus, all species become demographically, if not ecologically, equivalent. Because the populations of all species are stabilized by density dependence, extinction can only follow upon broad-scale environmental change or evolution of species relationships. Thus, extinction takes place over the whole region rather than within local communities, and the time between events is brought onto the same scale as the production of new

species. Local interactions provide a driving force for ecological specialization and thus limit membership in local communities more stringently than the random sampling process inherent to Hubbell's model. However, local interactions do not set rigid upper limits to local diversity (community saturation) and thus diversity patterns are connected over a continuum between local and regional scales.

Shifts in the regional array of species as well as membership in local communities comes about through environment change, on one hand, and evolutionary changes in populations, on the other hand. The first of these influences drives diversity patterns externally while the second comprises internal drivers of diversity, potentially linking the species richness of a region to time. Evolutionary changes in populations have been postulated as causes of taxon cycles, referring to phases of expansion and contraction of populations ecologically and geographically (Wilson 1961; Ricklefs & Cox 1972; Ricklefs & Bermingham 2002). Ricklefs and Cox (1972) suggested that such cycles were driven by evolutionary interactions between consumer and resource populations (predator-prey, pathogen-host), which would result in a continual reshuffling of the distributions of species over the regional landscape. However, because the selective forces on these interactions are frequency dependent, favoring the consumer when it is rare, the end result

of such evolutionary-ecological dynamics rarely is extinction.

The relative importance of such intrinsic processes is revealed by the apportionment of most of the variance in population size or ecological and geographical distribution at low taxonomic levels (i.e., species within genera) (Ricklefs & Cox 1972; Brown *et al.* 1996; Gaston & Blackburn 1996; Gaston 2003). For example, 87% of the variance in the total population size and 85% of the variance in south-north (warm cold) midpoint position of European passerine birds resides at the level of species within genera (Scheuerlein & Ricklefs 2004). In contrast, 80% of the variance in position along a wet-dry habitat gradient resides at the level of genera within families, reflecting greater conservatism of habitat specialization. At a more local scale, 71% of the variance in abundance of trees on the 50-ha forest dynamics plot on Barro Colorado Island (BCI), Panama, resides at the level of species within genera, with an additional 22% among genera within families. According to Hubbell's mutation model of speciation (Hubbell 2001), population size has no heritability and all its variance should occur only on the level of species within genera, as shown for the randomized BCI data in Table 2. Thus, relative abundances do carry a phylogenetic signal, most likely arising from variation in ecological relationships of taxa to their environments.

Clearly distribution and abundance are highly labile, but do not closely match adaptations of trophic ecology or habitat specialization that are conserved at higher taxonomic levels. Reasonable candidates driving this variance are relationships with consumer and resource populations, although more conservative attributes of species-environment relationships also might be important. Indeed, the influence of some extrinsic drivers, such as global climate change, on species distribution and abundance are more likely to be expressed

at higher taxonomic levels, reflecting common adaptations to environmental conditions and selective extinction. For example, late Tertiary extinctions of trees from Europe were concentrated in orders, such as the Laurales and Magnoliales, with primarily tropical distributions (Latham & Ricklefs 1993a; Svenning 2003).

Ecologists accept all the components of this regional view of diversity, including metapopulation dynamics, source-sink relationships, and mass effects within landscapes. Ecologists have also argued for an open community concept with species distributed more or less independently over ecological gradients within regions (Gleason 1926; Whittaker 1953). A considerable body of theory has developed around the problem of dispersal and habitat specialization in competitive systems (Holt 1996; Chesson 2000; Holt 2003). Why, then, have ecologists been reluctant to accept the influence of regional processes on local ecological systems and to make these processes a part of the ecological research paradigm? This inertia seems rooted in part on the practical scale of ecological investigation, which has not been able to deal with regional patterns and evolutionary time scales. The establishment of programs such as the 50-hectare plots and ancillary studies in tropical forests around the world (Condit 1995) is a wonderful initiative in the direction of producing comparable data on diversity on a global scale.

Another part of the inertia of local ecology has been the long tradition of local studies with homogeneous model systems or microcosms, which are valuable for exposing strong interactions but misleading with respect to the immense complexity of natural systems. Most community theory developed from a bounded community concept that could be described by a matrix of interactions and solved for the outcome of invasions by species with random attributes (Vandermeer 1969, 1972; May 1975; Roughgarden 1989). For the most part, these

studies did not account for spatial variation in the environment, except for the provision of refuge from predation (Werner & Hall 1976; Wellborn *et al.* 1996). Nor did they allow for evolution. For example, community invaders in natural systems are mostly well adapted to the local conditions and bear a close evolutionary relationship to species already present. Thus, they cannot be modeled as species having random interaction coefficients with others in the community (Roughgarden 1989; Morton *et al.* 1996). Invasion of local communities, which occurs through ecological and geographical expansion of the invading population, is supported by movement of individuals from productive populations elsewhere and often accompanied by evolutionary adjustment of the invading and resident species. Thus, while model systems are instructive in a general qualitative way, they overestimate the structuring influence of local interactions on communities relative to regional and evolutionary factors. I believe that in order for this attitude to change, ecologists must abandon local concepts of communities and regard (that is, design research with respect to) species interactions as playing out within regions. This will integrate a continuum of processes on scales from local to the entire region and ranging in time from the intervals between birth and death events to the intervals between speciation and extinction events.

Conclusions

The most important point to be made with regard to the generation and maintenance of patterns of biodiversity is that the concept of the community has no local validity. Species interactions play out over entire regions. Movement of individuals between habitats connects the locality to the broader region and links local and regional diversity. Because of habitat specialization, the competitive abilities of

species within whole regions are approximately equivalent and therefore competitive exclusion within a region is infrequent. Competitive equivalence is maintained by variation in habitat breadth; the resulting demographic equivalence of species places the time scale of extinction on the same order as that for species production. Thus, regional and historical factors shape the size of the regional species pool, and local diversity is sensitive to the size of the regional pool of species. To determine how large-scale processes have influenced diversity, ecologists must incorporate regional, historical, and phylogenetic perspectives in the design of biodiversity sampling across different spatial dimensions, environmental gradients, and regions.

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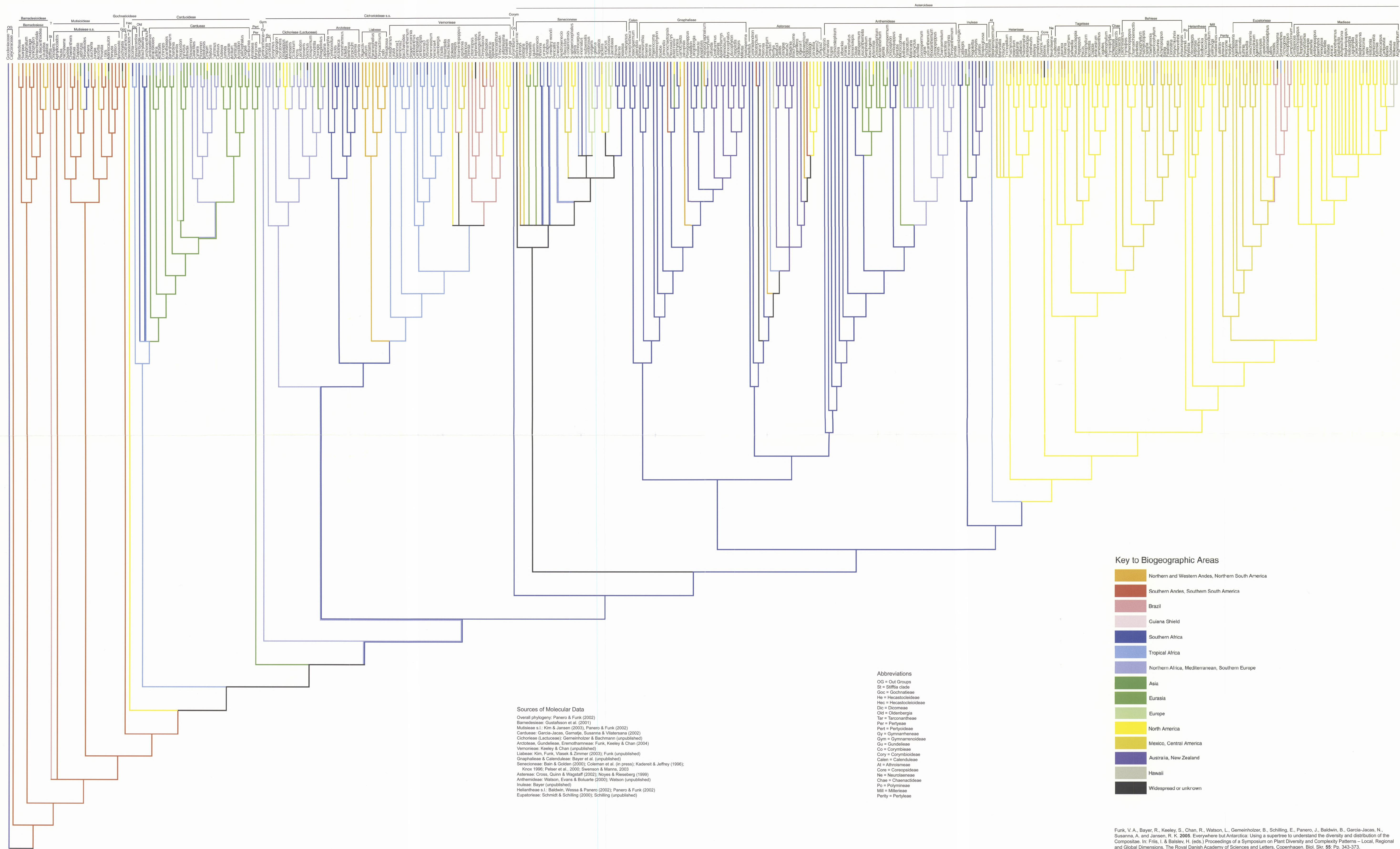


Fig. 4. A supertree of the Compositae, branches and internodes are colored according to the distribution of the terminal taxa or the optimization of those distributions. Abbreviations and references are listed at the base of the figure.

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