LOMOLINO, M.V. et al. 2006.
***Biogeography*. Ed. 3.**
Sinauer Associates, Sunderland.

HOW COMPLEX, REALLY, ARE BIOTAS? If the relationships among biotas in different areas of the world were mostly the product of either a simple vicariance or predictable dispersal history (e.g., via the progression rule), most of the many available methods would find the same general area cladogram and, given accurate phylogenies, it would not be particularly difficult to reconstruct the history of biotas. Let's look in some detail at an example of a system with a very simple geological history—the Hawaiian Archipelago. Waren Wagner and Vicki Funk (1995) edited an excellent book that brought together much of the phylogenetic and biogeographic research on the biota of the Hawaiian Islands, although a number of more recent studies of this biota are available as well (e.g., see Figure 11.9). Each chapter presented a cladistic and biogeographic analysis of a different group of organisms. In the final chapter, Funk and Wagner provided synthetic analysis of the biogeographic history of over 20 Hawaiian lineages, including such diverse groups as terrestrial invertebrates (insects and spiders), birds (honeycreepers), and flowering plants.

As we saw in Chapter 8, the Hawaiian Archipelago has a dramatically simple geological history resulting from the Pacific Plate drifting over a hot spot now located at the southeastern end of the island chain, currently beneath the island of Hawaii and another volcano (Loihi Seamount) to the southeast, which is growing but still submerged below the ocean (see Figure 8.20). The formation of the islands began 75 to 80 million years ago, but there may have been times since then when there was little or no emergent land. The oldest of the present major islands is Kauai, the northwestern-most island, which was formed about 5.1 million years ago. The ages of the islands decrease down the chain to the southeast: Kauai, Oahu, Molokai, Maui, and Hawaii.

Given this simple geological history, we can develop a relatively straightforward geological area cladogram (Figure 12.10) to use as a hypothesis of

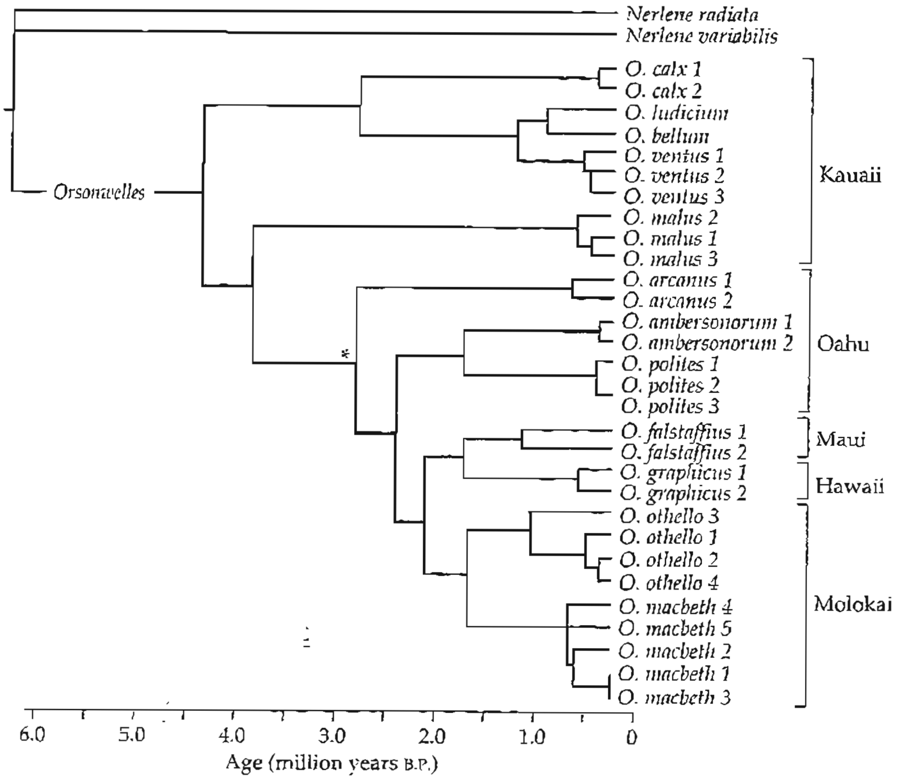
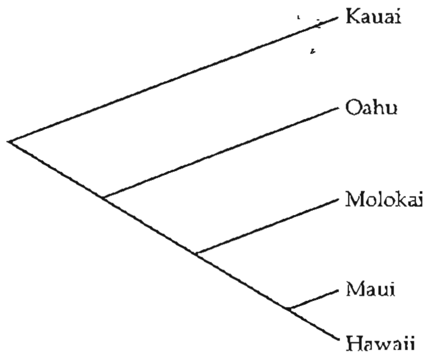


FIGURE 11.9 Phylogeny and estimated divergence times derived from molecular data for 12 of the 13 known species of the endemic Hawaiian linyphiid spider genus *Orsonwelles* (see Figure 12.13 for distributions). Branch lengths differed significantly in the original phylogeny such that a simple molecular clock could not be used to estimate divergence times. Therefore, a non-parametric rate smoothing procedure (Sanderson 1997) was used to estimate divergence times after calibrating the rates of divergence with the divergence event at the node marked by an asterisk, a geologically well-dated age of origination of the Koolau range in Oahu, and the point of separation of species on Kauai from those on all other islands. (After Hormiga et al. 2003.)

FIGURE 12.10 The area cladogram predicted for the Hawaiian Islands based on a simple progression rule. This is the pattern of phylogenetic relationships that would be expected if a lineage colonized each island in turn as it was formed by the emergence of a volcano from the sea.



taxon relationships under the following assumptions: that a taxon originally colonized either Kauai, the oldest present island, or an older island to the northwest of Kauai that is now submerged; and that, as newer islands were formed, each was colonized from an ancestral population on the adjacent and older island up the chain. This prediction should look very much like the progression rule we discussed earlier in this chapter (and shown in Figure 7.12B), and is one process that would lead to a high level of congruence across the codistributed lineages analyzed by Funk and Wagner. Deviations from this predicted pattern could, however, result from back-colonization from younger to already inhabited and older islands, from colonization of non-adjacent islands (which could also be interpreted as extinctions of populations on islands in between), from in situ speciation on a single island (which might occur via sympatric or microallopatric modes), or from more recent colonization of the archipelago itself.

So what do the results of the phylogenetic and biogeographic analyses show? The bottom line is that the simple prediction generated from the geological area cladogram is not supported as a general rule. Instead, the distributions of the lineages studied show a rich variety of relationships with respect to their phylogenetic histories. We can present only some of this variety in a simplified form here (for the full story, read Wagner and Funk 1995 and more recent literature, including an interesting analysis of geological and colonization histories by Price and Clague 2002).

Some clades (e.g., *Drosophila* fruit flies, other invertebrates, and certain plants) do indeed show a more or less clear progression rule, with basal taxa on older islands and progressively more derived forms on younger islands (Figure 12.11A,B; Figure 11.9). But other clades show very different patterns. One variation, found in the closely related plants *Schiedea* and *Alsinidendron*, is a series of subclades, each exhibiting its own progression rule with multiple waves of dispersal from older to younger islands (see Figure 12.11C). A clear exception to any progression rule is found in the plant genus *Tetramolopium* (see Figure 12.11D), in which the ancestral species clearly colonized one of the younger islands (either Hawaii or Maui) and subsequently dispersed to older ones (Oahu and Molokai), but apparently never reached the oldest (Kauai). Several other cladograms show complex patterns that clearly do not support a progression rule (e.g., the honeycreepers in Figure 12.12A, which have sister taxa on islands of contrasting age: Kauai and Hawaii), while still others are not easily resolved, and could be interpreted to suggest two or more very different histories.

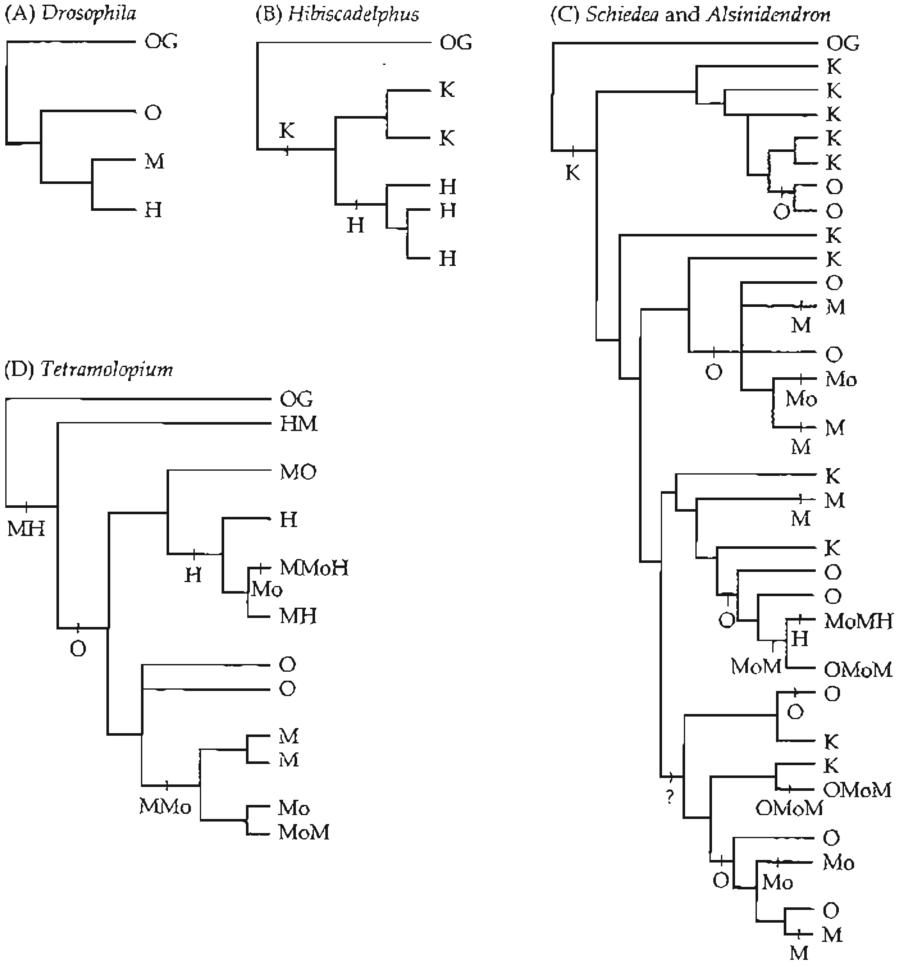
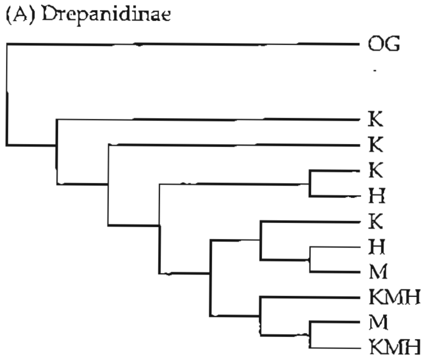


FIGURE 12.11 Area cladograms for four groups of Hawaiian organisms, simplified to include only the outgroup and those taxa found on the five largest islands. OG = outgroup; K= Kauai; O = Oahu; Mo = Molokai; M = Maui; H = Hawaii. Letters on the terminal branches (right) indicate present distributions; letters placed on the tree indicate over-water dispersal to colonize new islands; and multiple letters for the same island without multiple colonization events indicate within-island speciation events. (A) A group of *Drosophila* fruit flies shows a progression rule, with the more derived forms occurring on progressively younger islands. (B) The endemic plant genus *Hibiscadelphus* shows a highly modified progression rule, with the more derived taxa occurring on the youngest island (Hawaii) and the ancestral taxa on the oldest island (Kauai), but with multiple speciation events within these two islands, and no occurrences on the islands of intermediate age. (C) The closely related endemic plant genera *Schiedea* and *Alsinidendron*. This group comprises four subclades, each of which shows a general progression rule. Note, however, that there have also been multiple independent colonizations of the same island (e.g., Oahu, six times) and speciation events within islands (e.g., especially on Kauai and Oahu). (D) The plant genus *Tetramolopium*, which is probably a fairly recent immigrant to the archipelago, shows no evidence of a progression rule. It originally colonized either Maui or Hawaii, and subsequently dispersed to Molokai and Oahu, but apparently never got established on the oldest island, Kauai. (After Funk and Wagner 1995.)



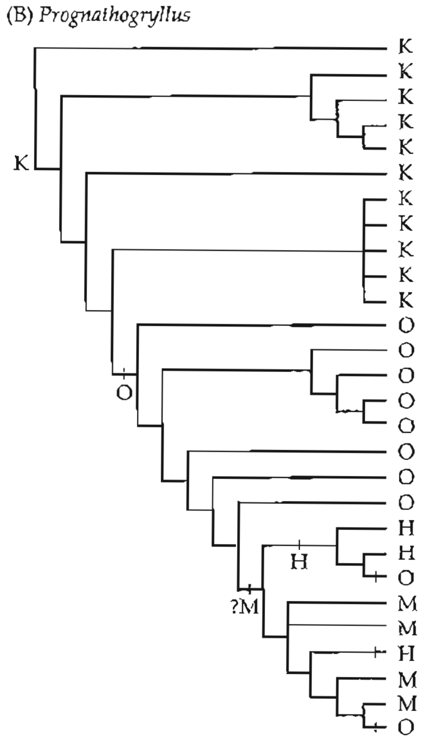


FIGURE 12.12 Area cladograms for two lineages of animal groups endemic to the Hawaiian archipelago and showing contrasting patterns of colonization and speciation. Localities and colonization events are coded as in Figure 12.11. (A) The Hawaiian honeycreepers of the avian subfamily Drepanidinae show many episodes of interisland colonization followed by speciation in isolation on the different islands. The direction of colonization is not known for the honeycreepers because there have been so many colonization events that the direction of dispersal often cannot be resolved from patterns of phylogenetic relatedness. (B) The cricket genus *Prognathogryllus* shows relatively few interisland colonization events, but each such event has been followed by multiple episodes of within-island speciation. (After Funk and Wagner 1995.)

The cladograms also reveal many different patterns of colonization and speciation. The examples of progression rules mentioned above illustrate cases of dispersal from older to younger islands. But there are also many cases of colonization of older islands from younger ones. One example, also mentioned above, is the genus *Tetramolopium*. Another is the Hawaiian honeycreepers, in which several recently derived taxa occur on the oldest island, Kauai (see Figure 12.12A). Again, it is important to mention that, for several clades, it is difficult to pinpoint the island that was first colonized, and therefore it is equally difficult to determine the direction of subsequent dispersal events that resulted in the colonization of additional islands. Such problems may be due to difficulty in resolving the cladograms, but they may also be due to unresolvable complications in the biogeographic history. For example, branches of lineages that went extinct on islands at different times in the past and did or did not colonize other islands and leave descendants there, can make it difficult to reconstruct the biogeographic history even though the phylogenetic reconstruction may be well resolved and accurate.

With respect to speciation, the cladograms do show examples of allopatric speciation presumably caused by dispersal to—and differentiation, on—different islands. Perhaps the best example is that of the honeycreepers (see Figure 12.12A). In general, the most closely related pairs of species occur on different islands, and often these islands are far from each other (e.g., Kauai and Hawaii, at opposite ends of the archipelago). This pattern of lineage diversification as a result of repeated episodes of colonization and speciation fits well with that seen in other groups of birds in other archipelagoes, such as the Galápagos and East Indies. On the other hand, the predominant pattern, seen in many clades of Hawaiian arthropods and plants, is one of extensive speciation and radiation within islands (see Figure 12.12B). This is very similar to the pattern observed in groups of fishes and mollusks in lakes such as those of Africa's Rift Valley (see Chapter 7). Further, since we know the ages of the Hawaiian Islands, we can estimate the minimum times for various speciation events. Clearly, all of the within-island speciation occurred within the last 5 million years, and some of it probably occurred (e.g., on Hawaii) within the last 500,000 years (Table 12.3).

It is important to note, however, that just because speciation occurred *within* an island and not just among islands, geographic isolation still may have played an important role in the differentiation of the populations. All of the large Hawaiian islands have a great deal of topographic relief and habitat heterogeneity including mountain ranges, large rivers, and other land features that may serve as barriers to dispersal. For organisms that disperse as poorly as some insular plants and invertebrates, this topographic heterogeneity promotes **microallopatric** speciation and rapid divergence and adaptive radiation among populations inhabiting the diversity of environments found on these

TABLE 12.3 *Estimated ages of the most recent common ancestors (MRCA) of some Hawaiian lineages*[a]

Lineage	Type of organism	Number of species	Age (Ma)	Source
Hawaiian fruitflies (Drosophilidae)	Insect	ca. 1000	26	Russo et al. (1995)
Hawaiian lobelioids (Campanulaceae)	Plant	125	15	Givnish et al. (1996)
Megalagrion damselflies (Coenagrionidae)	Insect	23	9.6	Jordan et al. (2003)
Silversword Alliance (Asteraceae)	Plant	28	5.1	Baldwin & Sanderson (1998)
Laysan duck, *Anas laysanensis* (Anatidae)	Bird	1	< 5	Fleischer & McIntosh (2001)
Hawaiian crows, *Corvus hawaiiensis* + other spp.? (Corvidae)	Bird	1 + ?	< 4.2	Fleischer & McIntosh (2001)
Hawaiian honeycreepers, Drepanidinae (Fringillidae)	Bird	ca. 50	4–5	Fleischer et al. (1998)
Viola spp. (Violaceae)	Plant	6	3.7	Ballard & Sytsma (2000)
Flightless Anseriformes, 'moa-nalos' (Anatidae)	Bird	4	< 3.6	Sorenson et al. (1999)
Hawaiian thrushes, *Myadestes* spp. (Muscicapidae)	Bird	5	< 3.35	Fleischer & McIntosh (2001)
Kokia spp. (Malvaceae)	Plant	4	< 3	Seelanan et al. (1997)
Flightless rails, *Porzana sandwicensis* + other spp.? (Rallidae)	Bird	1 + ?	< 2.95	Fleischer & McIntosh (2001)
Geranium spp. (Geraniaceae)	Plant	6	2	Funk & Wagner (1995)
Hesperomannia spp. (Asteraceae)	Plant	4	1.81–4.91	Kim et al. (1998)
Flightless ibises, *Apteribis* spp. (Plataleidae)	Bird	2	< 1.6	Fleischer & McIntosh (2001)
Hawaiian duck, *Anas wyvilliana* (Anatidae)	Bird	1	< 1.5	Fleischer & McIntosh (2001)
Flightless rails, *Porzana palmeri* + other spp.? (Rallidae)	Bird	1 + ?	< 1.05	Fleischer & McIntosh (2001)
Hawaiian geese, *Branta* spp. (Anatidae)	Bird	3	< 1	Fleischer & McIntosh (2001)
Hawaiian black-necked stilt, *Himantous mexicanus knudsenii* (Recurvirostridae)	Bird	1	< 0.75	Fleischer & McIntosh (2001)
Hawaiian hawk, *Buteo solitarius* (Accipitridae)	Bird	1	< 0.7	Fleischer & McIntosh (2001)
Tetramolopium spp. (Asteraceae)	Plant	11	0.6 – 0.7	Lowrey (1995)
Metrosideros spp. (Myrtaceae)	Plant	5	0.5 – 1.0	Wright et al. (2001)

[a] Refer to Price and Clague 2002 for methods used to calculate divergence times. Note that several lineages are older than the oldest present large island (Kauai, 5.1 million years old), suggesting an initial colonization of an older, now submerged island. The MRCA of other lineages is considerably younger, implying relatively recent colonization events.

large islands (Figure 12.13). Nevertheless, the high frequency of speciation within islands, like that within lakes, raises other important questions about the role of ecological and genetic processes in speciation—and especially about the relative importance of geographic isolation and divergent selection pressures.

THE PERILS OF IGNORING TIME. We have seen in the Hawaiian example that, even in a region with a comparatively simple geological history, phylogenies for co-distributed lineages can generate a diversity of incongruent area cladograms, owing to a complex history of dispersal, vicariance, extinction, and speciation

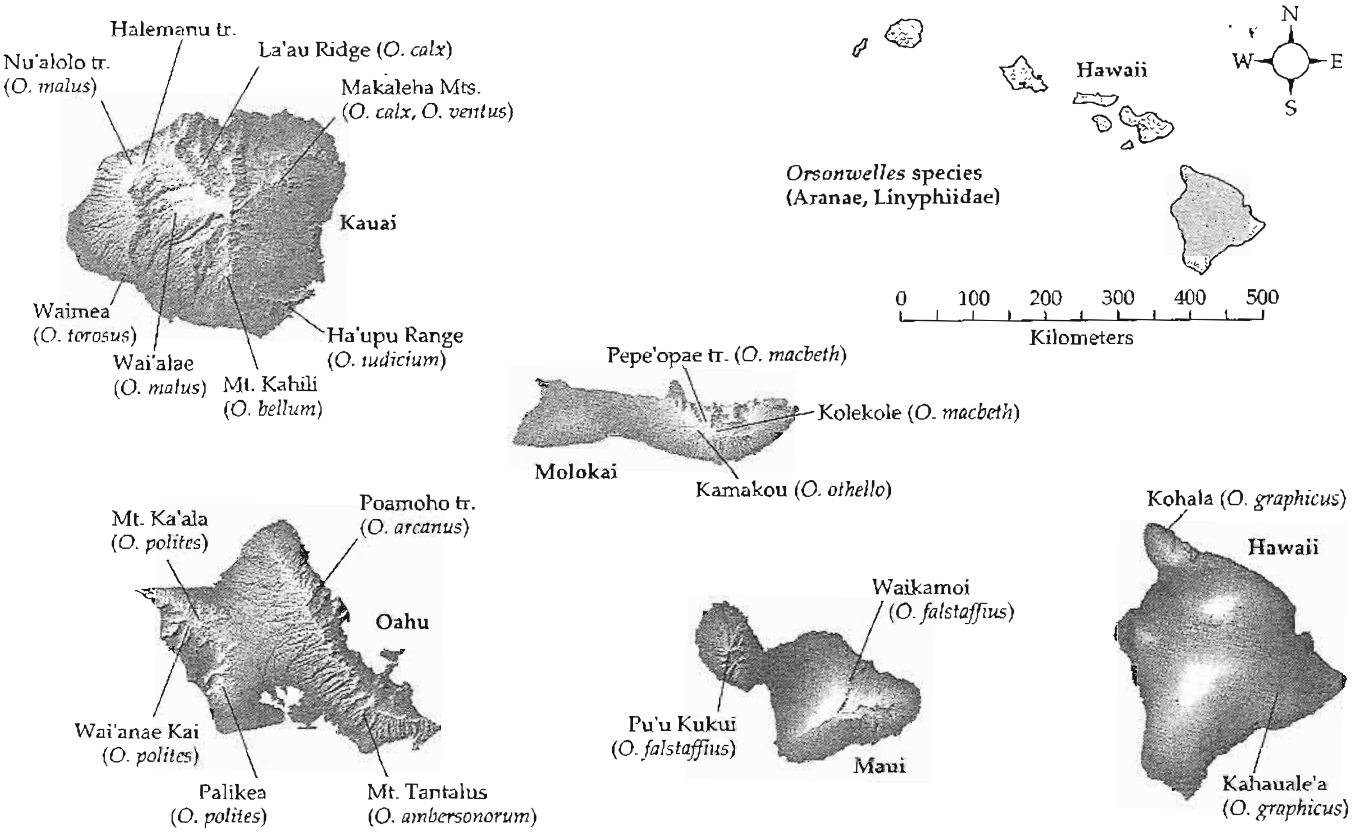


FIGURE 12.13 The geographic distribution of species of *Orsonwelles* spiders across the Hawaiian Islands. Although phylogenetic reconstructions suggest that a number of speciation events occurred within a single island, there is only one case of a completely sympatric distribution (*O. calx* and *O. ventus* in the Makaleha Mountains of Kauai). Even here, the phylogeny is indecisive about whether this is a result of a sympatric mode of speciation (followed by dispersal and divergence between *O. ventus* and the ancestor of *O. bellum* + *O. ludicium*), or of dispersal in the opposite direction resulting in secondary sympatry. Because of the allopatric distributions of all other species on different mountains, a microallopatric speciation mode is generally more likely than sympatric speciation. (After Hormiga et al. 2003.)

within and among areas. Yet, even if we found perfect congruence across a set of area cladograms, leading us to the provisional conclusion that all lineages shared a single history of simple vicariance, we may still have arrived at the wrong conclusion. Comparisons of area cladograms such as those in Figure 12.14 may appear to be relatively straightforward, but only for those clades that diversified at roughly the same times (i.e., the left side of Figure 12.14). Either the divergence events are both topologically and temporally congruent (upper-left box), indicating that the two lineages share a single biogeographic history; or they are geographically incongruent (lower-left box) indicating that they do not share the same history. However, the patterns shown in the boxes in the right of this figure (i.e., those for clades that diversified at different times) are likely to lead us to the wrong conclusions, unless of course our approach explicitly incorporates this asynchrony in clade diversification. Note that the two clades in the upper-right comparison appear to exhibit perfect topological congruence, yet this is an artifact of not incorporating differences in divergence times for these lineages. Without accurate information on tem-

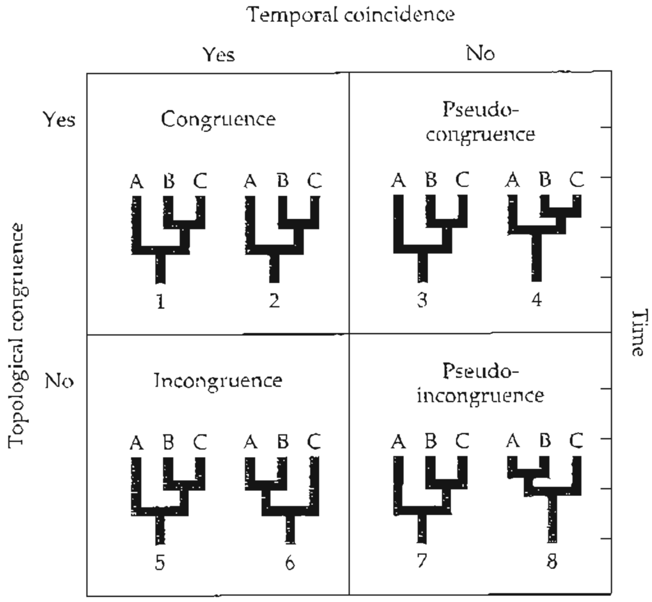


FIGURE 12.14 Four hypothetical sets of area cladograms for two lineages distributed across three areas (A, B, and C) in each comparison. See text for discussion. (After Donoghue and Moore 2003.)

poral coincidence of different clades, such patterns of cryptic biogeographic incongruence (called **pseudo-congruence**; Cunningham and Collins 1994) may generate erroneous conclusions about colonization history and evolution of these lineages (Hunn and Upchurch 2001). On the other hand, as more and more molecular phylogenies incorporate robust estimates of divergence times (see the discussion on molecular clocks in Chapter 11), we may discover that pseudo-congruent patterns are relatively common in parts of the world that have experienced temporally layered cycles of formation and erosion of dispersal barriers—first isolating, then allowing movement of a succession of lineages between the same set of areas (Donoghue and Moore 2003; see Figure 12.15).

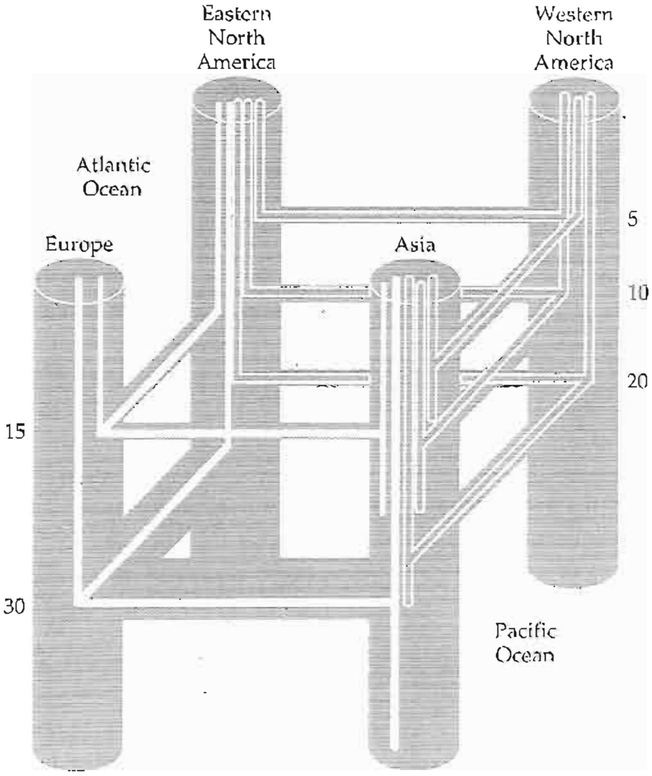


FIGURE 12.15 A depiction of area cladograms that summarizes historical tracks inferred from phylogenetic analyses of seven plant lineages distributed across four Northern Hemisphere areas of endemism. Each track traces one of two postulated intercontinental dispersal routes: either a Beringian route across the Pacific Ocean—with evidence presented here of having dispersal routes forming at three different timeframes (numbers are in millions of years); or a North Atlantic route—with two different timeframes for dispersal shown here. The temporal component of this complex biogeographic history was inferred by estimating divergence times from molecular phylogenies, and demonstrates "pseudo-congruence" embedded within topologically congruent sets of area cladograms. (After Donoghue and Moore 2003.)

7

What Are We Learning about Biotic Histories?

This chapter began with an extended discussion of historical biogeography during the early- to mid-twentieth century. This period was dominated by a tradition of using one or more criteria (see Table 12.1) to "locate" a center of origin, generally in the Northern Hemisphere, and to propose scenarios for the dispersal of species away from that center, sometimes including untested notions of waves of derived species supplanting more primitive forms as they advanced out of the center. The death knell for this approach was two-pronged—Croizat's panbiogeography, with its emphasis on discovering the general patterns of distribution on one hand; and Hennig's phylogenetic methods, with its insistence on discovering monophyletic groups and the ancestor-descendant cladogenetic sequence, on the other hand. Brundin applied both methods in his classic study in the late 1960s and interpreted his results with the benefit of the recent revelations of plate tectonic theory. The 1970s saw the remolding of phylogenetics and track analysis into a form of biogeography that narrowed the field to a search for the general vicariant backbone shared by a set of taxon-area cladograms.

TABLE 12.1 *Criteria used and abused for indicating center of origin of a taxon*

1. Location of greatest differentiation of a type (greatest number of species)
2. Location of dominance or greatest abundance of individuals (most successful area)
3. Location of synthetic or closely related forms (primitive and closely related forms)
4. Location of maximum size of individuals
5. Location of greatest productiveness and relative stability (of crops)
6. Continuity and convergence of lines of dispersal (lines of migration that converge on a single point)
7. Location of least dependence on a restricted habitat (generalist)
8. Continuity and directness of individual variation or modifications radiating from the center of origin along highways of dispersal (clines)
9. Direction indicated by geographic affinities (e.g., all Southern Hemisphere)
10. Direction indicated by the anuual migration routes of birds
11. Direction indicated by seasonal appearance (i.e., seasonal preferences are historically conserved)
12. Increase in the number of dominant genes toward the centers of origin
13. Center indicated by the concentricity of progressive equiformal areas (i.e., numerous groups are concentrated in centers, and numbers decrease gradually outward)

Source: After Cain (1994).

While most of today's historical biogeographers find this adherence to "vicariance only" unnecessarily and unrealistically narrow, vicariance biogeography provided a conceptual and methodological foundation for many of the approaches we use today, including those that incorporate methods to estimate dispersal, sympatric speciation, and extinction (see Table 12.2). Finally, from the arenas of molecular evolution and population biology, phylogeography emerged two decades ago and continues to mature into a remarkably popular aspect of modern historical biogeography.

Clearly, historical biogeography has experienced a series of important transformations over the past half century. Yet, until relatively recently, precious few data sets were available for addressing the history of terrestrial and marine biotas, and a good deal of the effort in historical biogeography focused on the "performance" of different approaches using exemplar data sets; most notable among these was Donn E. Rosen's (1978, 1979) poeciliid fish genera, *Heterandria* and *Xiphophorus*, from the uplands of Guatemala. Fortunately, all this changed with key technological advances of the past decade, including the increasing ease of obtaining DNA sequence and other forms of molecular data; the analytical power of sophisticated phylogenetic, population genetic, and biogeographic algorithms; and the availability of data from multiple co-distributed taxa, providing opportunities for exactly the kinds of comparative investigations required to sort general from individualistic biogeographic histories. These breakthroughs have greatly enhanced the analyses of biotic histories in both terrestrial and marine systems—covering a wide range of "deep" as well as "shallow" timeframes, and comparisons of biotas within, as well as among, the continents and island archipelagoes as well. The burgeon-

TABLE 12.2 *A selection of the more historically important or currently popular approaches and methods in historical biogeography*[a]

Approaches	Goal and selected methods	Original authors and general references
Descriptive biogeography	Comparing species lists	Sclater 1858 Hooker 1844–60
Evolutionary biogeography	Center of origin-dispersal	Matthew 1915; Cain 1944
Phylogenetic biogeography I	Phylogenetic systematics	Hennig 1966; Brundin 1966
Ancestral areas analysis	Area(s) of origin prior to dispersal	Bremer 1992; 1995
	Weighted ancestral areas analysis	Hausdorf 1998
Panbiogeography	Generalized tracks on a dynamic Earth	Croizat 1958
	Track analysis	Croizat 1958
Cladistic (Vicariance) biogeography	Vicariance on a dynamic Earth	Nelson 1974
	Reduced area cladogram	Rosen 1978
	Component analysis (CA)	Nelson and Platnick 1981; Humphries and Parenti 1999
	Three-area statement (TASS)	Nelson and Ladiges 1992
	Paralogy-free subtrees	Nelson and Ladiges 1996
Phylogenetic biogeography II	Vicariance, dispersal, geography of speciation	Wiley 1980
	Brooks parsimony analysis (BPA)	Wiley 1980
	Primary and secondary BPA	van Veller and Brooks 2000; Brooks et al. 2001
Parsimony analysis of endemicity (PAE)	Natural distribution patterns of taxa	B. Rosen 1988
	Areas of endemism	Craw 1988a; Morrone 1994
Event-based methods	Benefit/cost modeling of events	Ronquist and Nylin 1990
	Dispersal-vicariance analysis (DIVA)	Ronquist 1997
	Parsimony-based tree fitting	Page 1994; Ronquist 2002
Phylogeography	Geography of genealogical lineages	Avise et al. 1987; Avise 2000
	Phylogeny of gene trees	various
	Nested clade analysis	Templeton et al. 1995; Templeton 2004
	Coalescent-based approaches	various; Knowles 2003
	Comparative phylogeography	Zink 1996; Arbogast and Kenagy 2001

Source: After Crisci et al. 2003.

[a] This list differs primarily from Crisci et al. (2003) by distinguishing older and newer uses of "phylogenetic biogeography" as I and II, respectively, and separating the latter from cladistic biogeography.

ing number of publications from these studies is both encouraging and sometimes daunting, with the number and sophistication of publications increasing each year (e.g., see recent issues of these and other journals: Evolution, Journal of Biogeography, Molecular Ecology, Molecular Phylogenetics and Evolution, Biological Journal of the Linnean Society, Proceedings of the Royal Society of London, and Systematic Biology).

Earlier in this chapter and elsewhere in this book (Chapters 7 and 11) we featured a variety of examples of modern, molecular-based, biogeographic analyses of either single lineages or multiple co-distributed taxa (e.g., for the Hawaiian Archipelago). Here, we highlight a handful of intriguing studies that integrate information from a number of co-distributed taxa and demonstrate how modern historical biogeography is poised to produce synthetic and, in many cases, perhaps surprising insights about the histories of biotas.

Biotic Histories in Gondwanaland

From the beginning of modern historical biogeography, the plate tectonics model gave biogeographers one very clear exemplar system that should demonstrate a history of vicariance—the breakup of the continent of Gondwanaland. The timing and sequence of fragmentation of landmasses from the ancient Gondwanan continent is well known and provides for the construction of a geological area cladogram that offers explicit predictions about the topology of taxon-area cladograms for lineages that diversified in accordance with a vicariance model (see first Figure in Box 12.1). These lineages would have included the ratite and allied birds in the subclass Paleognathae, the chi-

BOX 12.1 *Defining and delineating areas of endemism*

In Chapter 10, we discussed the concept of endemism in detail and its importance in biogeography. In historical biogeography, an area of endemism is generally considered as the fundamental unit of analysis in cladistic-based approaches. Several decades of historical biogeography have been developed upon the premise that "the most elementary questions of historical biogeography concern areas of endemism and their relationships" (Nelson and Platnick 1981). Clearly, the importance of understanding relationships among areas, based on the taxa that occupied them, was associated with the idea that vicariance, followed by "allopatric speciation mode I" (see Figure 7.10) would produce congruent relationships across co-distributed taxa (see Figure 12.8).

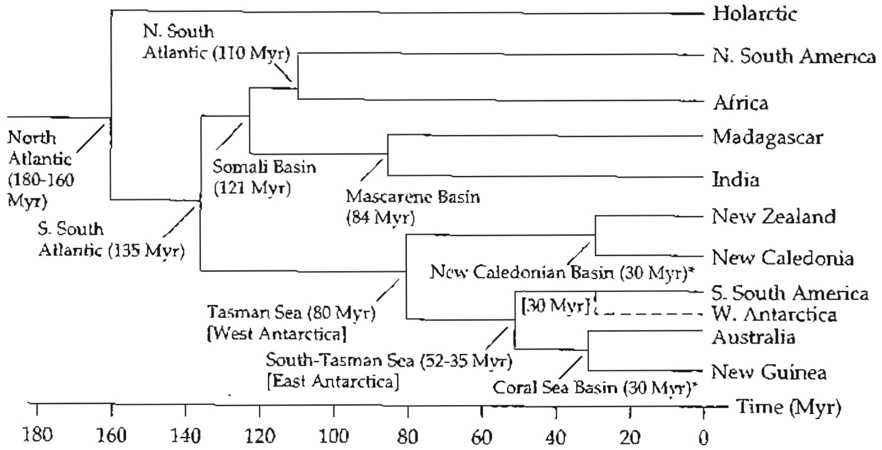
Delimiting areas of endemism would seem to be an easy thing to do. After all, at the simplest level, they merely represent geographic areas where two or more endemic taxa share overlapping, or congruent, distributions. But we know that it is rare that the distributions of two or more taxa overlap exactly, except in cases where distributional limits are set by very discreet abiotic boundaries (e.g., lakes or islands), and biogeographers still are debating how to define and delineate them. How much or how little overlap in ranges, or sympatry, should we accept in order to delimit an area of endemism? Or should some criterion other than sympatry be applied? Recently proposed definitions emphasize one of three criteria to define an area of endemism: (1) degree of distributional overlap, or sympatry; (2) barriers between separate areas resulting from vicariance; and, (3) as an operational extension of the latter, phylogenetic congruence between co-distributed taxa and their sister-taxa in the area on the other side of the barrier. For example:

Platnick's defintion. "At the minimum, it would seem that an area of endemism can be defined by the congruent distributional limits of two or more species. Obviously 'congruent' in this context does not demand complete agreement on those limits, at all possible scales of mapping, but *relatively extensive sympatry* (italics added) at some scale must surely be the fundamental requirement" (Platnick 1991; see also Morrone and Crisci [1995]; Linder [2001]).

Hausdorf's definition. "Areas of endemism can be defined as areas *delimited by barriers* (italics added), the appearance of which entails the formation of species restricted by these barriers" (Hausdorf 2002).

Harold and Mooi's definition. An area of endemism is "a geographic region comprising the distribution of *two or more taxa that exhibit a phylogenetic and distributional congruence* and having their respective relatives occurring in other such-defined regions" (Harold and Mooi 1994).

So, the definition of an area of endemism can range from requiring extensive sympatry (Platnick's definition) to little or none, with the main criterion being derived from a vicariance model of barrier formation and subsequent speciation (Hausdorf's and Harold and Mooi's definitions). The approaches to delineating areas of endemism are equally diverse, ranging from strongly geopolitical (e.g., "historically persistent Gondwanan landmasses according to paleogeographic reconstructions" [Sanmartin and Ronquist 2004] see figure below), to the quadrat approach of Morrone (1994) using Parsimony Analysis of Endemicity (PAE) to delineate areas of endemism based on the distributions of taxa within a region.



(*) alternative reconstructions date these events between 70–60 million years B.P.

In the Gondwanan example, the approach to delimiting areas would be an example of using Hausdorf's definition, because the appearance of barriers following the fragmentation of Gondwana into separate landmasses is a more important criterion than the "extensive sympatry" of any taxa at smaller scales within each landmass. The areas delimited based on this criterion are:

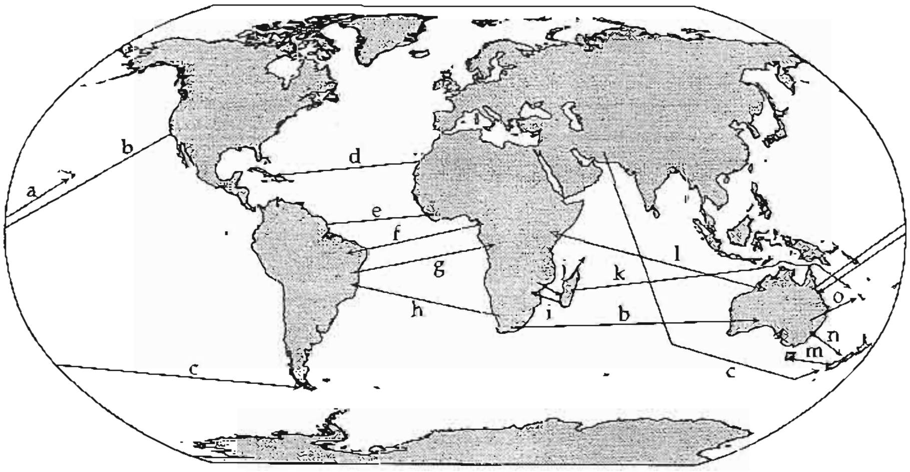
- Africa, south of the Sahara
- Madagascar, including several Indian Ocean islands
- India, including Nepal, Tibet, and Sri Lanka
- Australia and Tasmania
- New Zealand, including subantarctic islands on the same continental block
- New Caledonia
- New Guinea, including the Solomon and New Hebrides islands
- Southern South America
- Northern South America

These areas of endemism are informative to historical biogeographers because they have arisen from a well-understood sequence of historical fragmentation of Gondwana landmasses (see figure), which forms a basis for addressing the relative importance of vicariance and dispersal in the biogeographic history of these regions.

In many cases, however, the physical discreetness between areas is not so clear-cut, and so other methods need to be employed to delineate areas of endemism. A number of approaches and methods have been proposed (as examples, see Morrone 1994; Linder 2001), ronomid midges studied by Brundin, the southern beeches (*Nothofagus*), and a number of lineages of fishes and reptiles.

What evidence could we use to reject vicariance in favor of dispersal for any of these Gondwanan lineages? First and most obvious, taxon-area cladograms that are incongruent with the geological area cladogram would provide a reason to reject vicariance in favor of dispersal. Second, as we discussed in Chapter 11, molecular data could be used to estimate the absolute and relative times of divergence, and would provide a strong argument against vicariance if an estimated divergence time was younger than the time of area fragmentation.

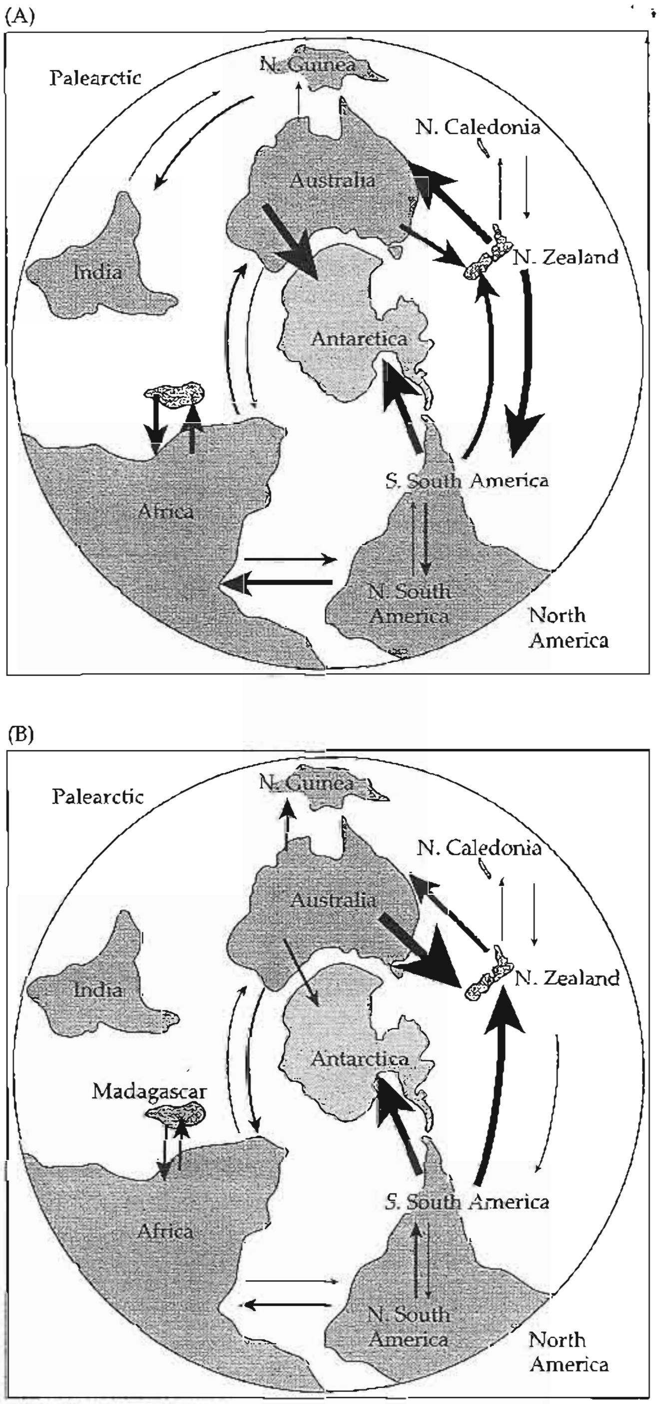
The results of a number of recent analyses are pointing to a surprising result—that transoceanic dispersal has played a far greater role in the biogeographic history of the Southern Hemisphere than had been predicted from the Gondwanan vicariance model. de Queiroz (2005) summarized many examples of disjunctions of a broad range of organisms, including primates, chameleons, frogs, and many genera of plants, distributed among landmasses across the Earth, many of Gondwanan origin (Figure 12.21). In each case, the disjunct distributions between sister taxa were interpreted as products of transoceanic dispersal, based on incongruence between molecular-based estimates of divergence times and geological estimates of the ages of fragmentation of landmasses. In another study, Sanmartín and Ronquist (2004) used a large data set, including 54 animal (insects, fish, reptiles, and mammals) cladograms and 19 plant taxon-area cladograms in a parsimony-based tree fitting analysis. Their analyses indicated that, overall, animal distributions are more



a *Scaevola* (Angiospermae: Goodeniaceae, three episodes of dispersal)
b *Lepidium* (Angiospermae: Brassicaceae)
c *Myosotis* (Angiospermae: Boraginaceae)
d *Tarentola* geckos from Africa to Cuba
e *Maschalocephalus* (Angiospermae: Rapateaceae)
f monkeys (Platyrrhinii)
g melastomes (Angiospermae: Melastomataceae)
h *Gossypium* (Angiospermae: Malvaceae)
i chameleons, three episodes of dispersal
j several frog genera
k *Acridocarpus* (Angospermae: Malpighiaceae)
l Baobab trees (Angiospermae: Bombacaceae)
m 200 plant species
n many plant taxa
o *Nemuaron* (Angiospermae: Atherospermataceae)

FIGURE 12.21 Examples of trans-oceanic dispersal, derived mainly from recent molecular phylogenies with estimates of divergence time. The strongest case for dispersal rather than vicariance is made when the phylogeny suggests a divergence date between two lineages that is much younger than predicted from a geological area cladogram, such as that shown in Box 12.1 for Gondwana. Arrows on lines indicate direction of dispersal; a line with two filled arrows indicates bi-directional dispersal; and unfilled arrows indicate uncertainty about direction. (After de Queiroz 2005.)

FIGURE 12.22 Analysis of historical dispersal events between major landmasses of Gondwanaland, inferred from a parsimony-based analysis of (A) 54 animal, and (B) 19 plant cladograms. The width of the arrows is proportional to the frequency of a particular route (details of analysis provided in original reference). For the animals in (A), the thick arrows connecting Australia and southern South America via Antarctica, as well as the one connecting New Zealand and southern South America, are consistent with the vicariance model of area fragmentation (see first figure in Box 12.1), suggesting that "dispersal" between these areas occurred prior to the break-up of the ancient continent. However, one could argue the same thing for the high frequency of Madagascar and Africa dispersals, but many of these are now considered to have resulted from post-vicariance dispersal events (see discussion in text and Figure 12.23). For the plants in (B), the signal of transoceanic dispersal is stronger than for animals, particularly in the very high frequency of dispersal from Australia to New Zealand, clearly incongruent with the geological cladogram. Note also the weak connections between northern and southern South America, the latter having much stronger historical affinities with other southern landmasses. (After Sanmartín and Ronquist 2004.)



congruent with the fragmentation sequence of Gondwanaland than are those of plants (Figure 12.22). A dramatic case of incongruence in plants, for example, involves the modern flora of New Zealand, which may have originated in large part, if not in total, via long-distance dispersal following the near disappearance of exposed land in New Zealand during the Oligocene (37–23 million years B.P.; Pole 1994; Winkworth 2002). Generally, their results suggest that plants have dispersed more frequently and more recently than animals among landmasses in the Southern Hemisphere. But even in animals, with their better overall fit to a Gondwanan vicariance model (see Figure 12.22), several long-held presumptions about purely vicariant histories appear to be inconsistent with molecular estimates of divergence dates. For example, divergence dates between African and Malagasy chameleons (Raxworthy et al. 2002), frogs (Vences et al. 2003), plants (Renner 2004), primates (Yoder et al. 2004), and carnivores (Yoder et al. 2003; Figure 12.23) appear to be much younger than the geological estimate of about 120 million years B.P. for the separation of Africa from a Madascar-India landmass. This appears to be strong evidence for a history of multiple colonization events between Africa and Madagascar via sweepstakes dispersal, rather than vicariance.

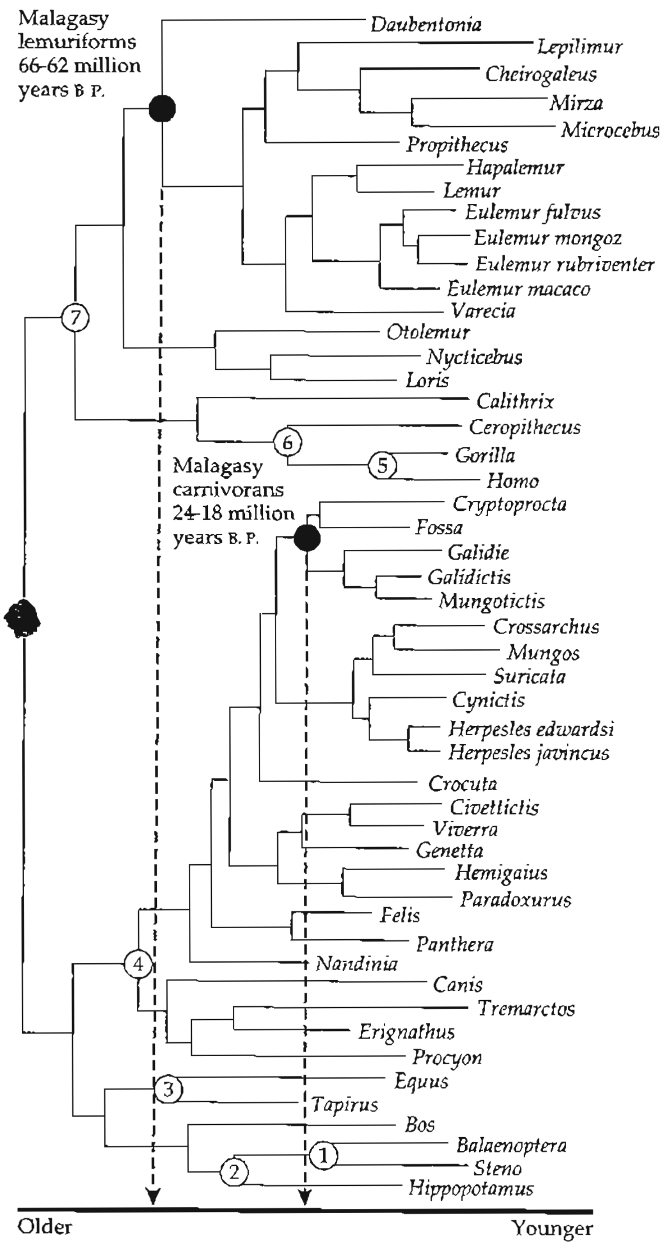


FIGURE 12.23 Molecular phylogeny comparing the ages of divergence of Malagasy primates (*Daubentonia*, the aye-aye; and a number of genera of lemurs) and carnivores (three genera of Malagasy 'mongooses'; *Fossa*, the Malagasy civet; and *Cryptoprocta*, the fossa). In each case, the Malagasy clade is monophyletic with a common ancestor at the black circle. Open circles with numbers are fossil-based calibration points used to estimate divergence times, which for the primates (66–62 million years B.P.) and carnivores (24–18 million years B.P.) post-date the geologically estimated time of separation of Africa and an ancestral Madagascar-India land mass (about 121 million years B.P.), and the separation of Madagascar from India (about 88 million years B.P.), suggesting colonization by ancestors of both clades by overwater "sweepstakes" dispersal. (After Yoder et al. 2003.)

We emphasize here the accumulating evidence of an important role for dispersal in the historical assembly of Southern Hemisphere biotas (McGlone 2005), but stress also that Sanmartín and Ronquist (2004) found congruence between some of their taxon-area cladograms and the geological cladogram, supporting vicariance as a component of biotic history as well. Interpreting the histories for any group of taxa can still be controversial (e.g., Briggs 2003; Sparks and Smith 2005).

We can mention two additional insights about the dynamic biogeography of Gondwanaland that have emerged from recent studies. The first provides substantial support for the reticulate nature of South America with Andean and southern parts of South America aligned historically with Australia and New Zealand, and northern (tropical) South America showing greater affinities to the Holarctic, and to some degree, Africa (see Sanmartín and Ronquist 2004; see Figure 12.22). This reticulated history formed the basis for Morrone (2002) subdividing South America into separate biogeographic regions (see Figure 10.16). Second, Gondwanaland appears to have played a surprisingly important role in the early diversification of a number of major groups of vertebrates previously thought to have originated in Laurasia, including neognathine birds (Cracraft 2001), ranid frogs (Bossuyt and Milinkovitch 2001; see Figure 7.11), placental mammals (Eizirik et al. 2001), and grasses (Bremer 2002).

Biotic Histories in the Holarctic

While the tectonic history of Gondwanaland can be summarized concisely into a geological area cladogram with a minimal number of area reticulations (first figure in Box 12.1), the geological history of connections and biotic interchange between Laurasian landmasses was much more complex throughout the Cenozoic. For example, although biogeographers have recognized only four broad areas of endemism for temperate deciduous forests—two in the Nearctic (eastern North America and western North America), and two in the Palearctic (Europe and eastern Asia; Figure 12.24A)—there has been a long history of debate about the historical sequence of connections between these areas. That these areas are likely to be highly reticulated is suggested by the inferred history of connections within and across the Holoarctic continents, summarized as follows:

1. Western and eastern Nearctic landmasses were separated by an epicontinental sea until the earliest Cenozoic epoch, the Paleocene (roughly 65 million years B.P.; see Chapter 8).
2. Multiple Beringian connections formed between the eastern Palearctic and western Nearctic landmasses during the Cenozoic (culminating in the important late-Pleistocene connections; see Chapter 9).
3. At least two Tertiary connections formed between the western Palearctic and eastern Nearctic across the North Atlantic (about 30 and 15 million years B.P., respectively).

The fossil evidence has previously been interpreted as demonstrating that ancient forests and taxa were widespread across Laurasia prior to its complex Cenozoic geological history, and that the current differences in species composition between areas is due primarily to extinction of ancestrally widespread taxa (Wolfe 1975; Tiffney 1985; Tiffney and Manchester 2001).

An increasing number of molecular phylogenetic data sets, many with estimates of divergence times, are becoming available for temperate deciduous forest plant and animal taxa distributed across the four recognized areas of

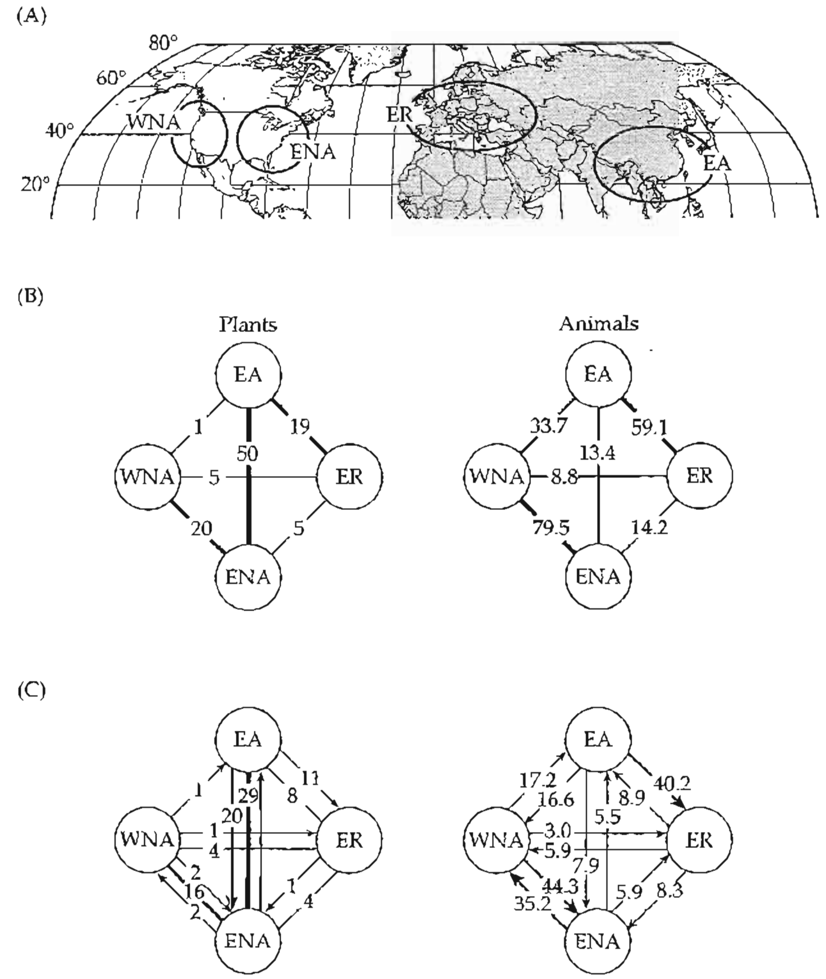


FIGURE 12.24 (A) Holarctic areas of endemism in plants and animals across eastern North America (ENA); western North America (WNA); Europe (ER); and Eastern Asia (EA). A comparison of disjunct patterns of distribution (B) and inferred ancestral areas and direction of movement (C), analyzed using animal data from Sanmartín et al. (2001). See text for discussion. (After Donoghue and Smith 2004.)

endemism. Donoghue and Smith (2004) used dispersal-vicariance analysis to compare taxon-area cladograms from 66 plant clades with the 57 animal clades analyzed by Sanmartín et al. (2001). As was the case in the Southern Hemisphere (Sanmartin and Ronquist 2004), the relative roles of dispersal and vicariance and patterns of dispersal among the Holarctic areas of endemism appear to differ between plants and animals, particularly in the historical relationship of eastern Asia and the Nearctic areas (as summarized in Figures 12.24B and 12.24C). That is, plants share a higher frequency of disjunct distributions of sister taxa between eastern Asia and eastern North America, and animals share more disjunction distributions between eastern Asia and western North America. Furthermore, again mirroring the Southern Hemisphere, there appears to be a higher frequency of more recent intercontinental dispersal events in plants than in animals in the Northern Hemisphere (but see Donoghue and Smith, 2004). Contrary to the "widespread ancient forest" model preferred by paleontologists, these and other studies support a history of multiple episodes of dispersal and vicariance between Palearctic and Nearctic areas during the Tertiary, primarily via a Beringian route (also supported in another study by estimated divergence dates on a molecular phylogeny for squirrels; Mercer and Roth 2003), but also to some degree via a Northern Atlantic route as well (see Figure 12.15).

Biotic Histories in, and Just Before, the Ice Ages

Phylogeographic—and particularly, comparative phylogeographic—studies have begun to reveal much about the responses of lineages and biotas to the dramatic climatic oscillations of the Pleistocene (Hewitt 2004). Yet, in a slightly expanded timeframe, many of the extant species and genera were also members of pre-Pleistocene, Pliocene, and Miocene biotas. We know that the Earth experienced dramatic geological and climatic changes during these epochs, including uplifting of mountains and plateaus, and closure of the Panamanian landbridge. Debate continues regarding the relative importance of Ice Ages versus earlier events on the origin of extant species and assembly of modern biotas (e.g., Johnson and Cicero 2004; Weir and Schluter 2004; Zink et al. 2004). Nevertheless, phylogeographic studies are clearly suggesting that the origination of many extant species and regional biotas date to pre-Pleistocene times, and are found in a wide range of biogeographic regions and biomes, including the tropical forests of northeastern Australia, central Africa, northern South America (Moritz et al. 2000), the Mexican Neovolcanic Plateau (Hulsey et al. 2003), the conifer forests of the Pacific Northwest in North America (Carstens et al. 2005), and the southwestern deserts of North America (Riddle et al. 2000; Zink et al. 2000; Riddle and Hafner, in press).

Within the Pleistocene, comparative phylogeography has provided interesting insights on the temporal cohesiveness of biotas across one or more glacial-interglacial climatic oscillations (reviewed by Hewitt 2004). For example, in the western Palearctic, biotas in Europe appear to have responded as cohesive subsets of taxa whose ranges retreated during glacial periods to one or more southern, unglaciated refugia (e.g. Iberian, Italian, Balkan), followed by northward range expansions following retreat of the glaciers (Figure 12.25). Often,

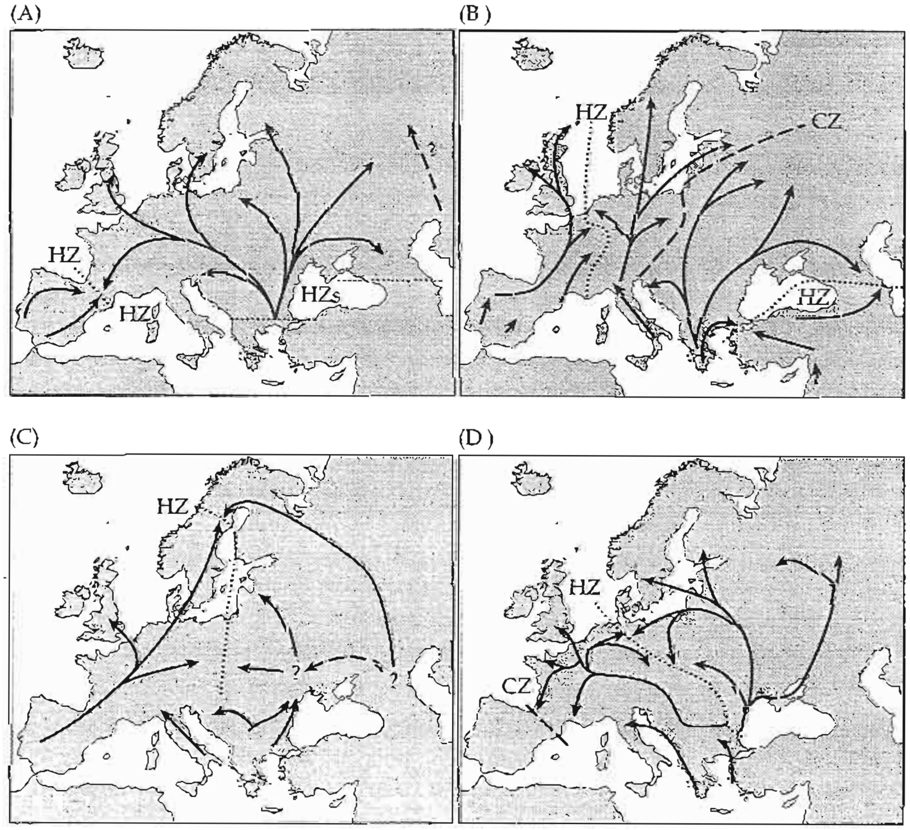


FIGURE 12.25 Four "paradigms" of postglacial colonization from Late Pleistocene southern refugia in the Palearctic as inferred from mtDNA phylogeographic studies. CZ and HZ are contact zones and hybrid zones, respectively, between lineages expanding from different refugia. The exemplars representing each of the four patterns here are for (A) the grasshopper (*Chorthippus parallelus*); (B) the hedgehog (*Erinaceus europaeus/concolor*); (C) the brown bear (*Ursus arctos*); and (D) the chub (*Leuciscus cephalus*). (After Hewitt 2004.)

separate "phylogroups" within a species can be recognized and assigned to a particular refugium, suggesting a history of isolation and divergence that extends deeper into the Pleistocene than just the latest of the 20 or so glacial-interglacial cycles. Farther to the east, Beringia served as a refugium for mammals, birds, plants, and invertebrates (Waltari et al. 2004), although the pattern of biotic responses appears to be more complex than has been the case in the western Palearctic (Hewitt 2004).

The Continuing Transformation of Historical Biogeography

As we close this chapter, and this unit of the book, we hope that it is clear that historical biogeography is rapidly blossoming into a productive and energetic discipline with the power to infer much about the geography of lineage and biotic diversification. We highlighted just a few studies demonstrating the tremendous progress being made in understanding the history of Earth's biotas, and we emphasized terrestrial systems, but recognize that much progress is being made in testing alternative hypotheses and elucidating the histories of marine biotas as well (e.g., Barber et al. 2000; Santini and Winterbottom 2002; Briggs 2003, 2004; Meyer et al. 2005). Although we discussed the fascinating biogeographic history of the Hawaiian Islands in some detail, we were unable to feature a growing number of other interesting studies of biogeographic and evolutionary experiments on oceanic archipelagoes (e.g., Cook et al. 2001; Emerson 2002; Heaney et al. 2005). Finally, we barely mentioned recent studies that are advancing the paleobiogeographies of long-extinct lineages, ranging from Paleozoic trilobites (Lieberman 2003, 2004) to Mesozoic dinosaurs (Upchurch et al. 2002).

Yet despite its great progress, especially in the past several decades, historical biogeography still has large hurdles to overcome if even more important advances are to be made. First, even though the large array of modern approaches illustrated throughout this chapter suggest that this is a discipline rich in theory and methods, historical biogeographers still are concerned about whether methods are sophisticated enough to unravel histories that are full of complexity, with reticulated biotas more often than not integrating multiple episodes of vicariance-driven speciation, dispersal, extinction, and sympatric speciation across timeframes spanning a few thousands to many millions of years of Earth's history. New methods continue to appear (e.g., Wojcicki and Brooks 2005), and what diverged to form distinct disciplines and methods are now merging into more synthetic approaches in which different methods are employed to address different questions at sequential stages in an analysis (Morrone and Crisci 1995; Althoff and Pellmyr 2002; Riddle and Hafner 2004, in press). Finally, along with continuing advances in methods, and growth in numbers and variety of lineages and biotas available for analyses, we are encouraged by recent calls for the re-integration of the historical biogeographic perspective into broader and more insightful ecological and evolutionary arenas (e.g., see Wiens and Donoghue 2004; summarized in Figure 15.36).

LOMOLINO, M.V. et al. 2006.
***Biogeography*. Ed. 3.**
Sinauer Associates, Sunderland.

John Wiens, a distinguished ecologist, and Michael Donoghue, an equally distinguished historical biogeographer, recently presented a conceptually broad and potentially insightful explanation for latitudinal gradients in species richness (Wiens and Donoghue 2004). They quite cogently argue the need for new syntheses—in this case, one drawing on the principles and insights of ecology, evolution, and biogeography. Counter to some prevailing assumptions of historical biogeographers, Wiens and Donoghue argue that ecological interactions and climatic conditions *are* important, but primarily through their influence on evolutionary and biogeographic processes—again, these being speciation, dispersal, and extinction. Their tropical conservatism hypothesis combines the insights and arguments of numerous earlier biogeographers and ecologists, but its integrative nature is even more compelling. For reasons discussed above and summarized in Table 15.4, speciation rates tend to be higher in the tropics. In addition, because the tropics include a larger portion of the Earth's surface area, and because tropical ecosystems are more stable, more predictable, and less harsh, extinction rates should be lower in the tropics. For these same reasons (i.e., the relatively stable, predictable, and benign nature of tropical environments), tropical species tend to adapt over time by becoming more specialized. Put another way, species adapted to the variable and sometimes unpredictable nature of high-latitude environments must have broad niches, which allow them to adapt in situ—or disperse to—other environments during inclement periods.

Latitudinal gradients in speciation and extinction rates described above explain how the pattern is established, but niche conservatism and its influence on ecological interactions and dispersal can explain why the pattern is maintained, and why it has intensified over time (see Figure 15.25). As David Janzen (1967) remarked in one of his classic papers, "mountain passes *are* higher in the tropics"—not because the mountains are actually taller, but because tropical species tend to have relatively narrow niches and, therefore, more limited abilities or propensities to disperse across high montane habitats to colonize other lowland forests. Although a small fraction of these tropical species may eventually colonize regions in the higher latitudes, their dispersal (immigration) rate is insufficient to compensate for the relatively low speciation rate and high extinction rates of temperate and high latitude ecosystems.

There are at least two interesting corollaries of Wiens and Donoghue's hypothesis (Figure 15.36). First, geographic ranges of many animals and plants seem to be limited along their higher-latitude boundaries by climatic factors, suggesting that cold climate and niche conservatism prevent many tropical lineages from invading the temperate zone. Second, many species exhibiting the predicted gradient in species richness also exhibit a complementary phylogeographic pattern—"with an origin in the tropics and more recent dispersal to temperate regions" (Wiens and Donoghue 2004:642; see Figure 15.36).

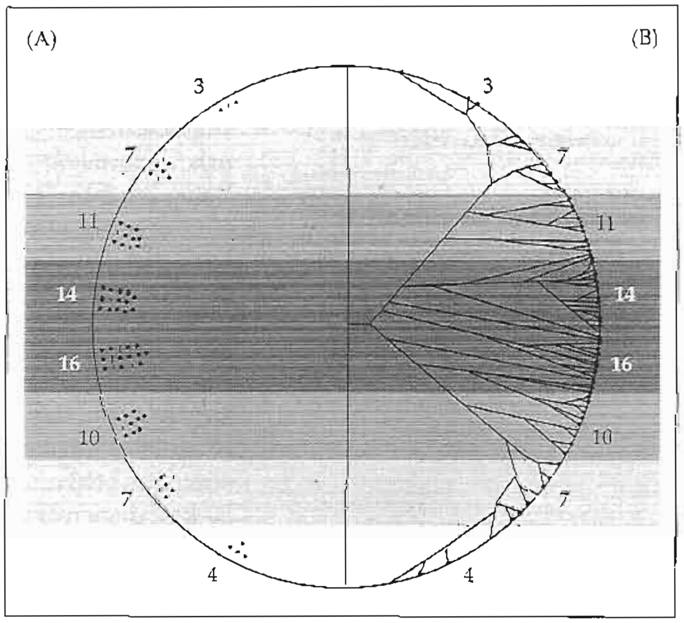


FIGURE 15.36 (A) Many earlier explanations for the latitudinal gradient in diversity were based on standard ecological approaches (see Table 15.4) and on correlations between species richness and an environmental variable (e.g., temperature or solar energy, represented here by intensity of shading). Here, each dot represents a different species, and the numbers along the Earth's surface represent species richness at that point. (B) In contrast, more integrative explanations for this general pattern are based on the history of lineages and of place, and how ecology, phylogeny, and adaptation have combined to determine the development and maintenance of biological diversity. Wiens and Donoghue's (2004) explanation is based, in part, on the tropical conservatism hypothesis (dots represent species, and lines connecting them represent both evolutionary relationships and simplified paths of dispersal). Because tropical climates are relatively benign, aseasonal, and predictable, their species tend to become ecologically specialized and limited in their abilities to disperse to other sites within the tropics or to those in the higher latitudes. Thus, because their species tend to be more isolated, and because the tropics tend to be larger and older than other biomes and regions, speciation rates and total number of species accumulated should be higher in the tropics. Wiens and Donoghue's hypothesis not only offers a synthetic explanation for this pattern, based on ultimate causes—speciation, extinction, and dispersal—but it also proposes other, testable predictions (e.g., that tropical lineages should, on average be relatively old, whereas those in temperate regions are often recently derived from the few clades that disperse from tropical regions). (After Wiens and Donoghue 2004.)

Wiens, J.J. & Donoghue, M.J. 2004.
Historical biogeography, ecology and species richness.

Box 1. Ecology and area cladograms

Ecology can be crucially important to historical biogeography, even if one's goal is only to reconstruct relationships among areas of endemism (i.e. cladistic biogeography). For example, area cladograms do not depend solely on the history of geological connections among areas, but instead on the history of connections among suitable habitats. It is easy to imagine cases where the history of connections among habitats in different areas differs from the history of geological connections (e.g. even though Mexico has always been geologically connected to North America, many of the lowland taxa in Mexico originated in South America, whereas many highland taxa originated in North America [1]).

Cladistic biogeography has considered primarily three processes in explaining biogeographical patterns: (i) vicariance; (ii) dispersal; and (iii) extinction [5–10]. Generally, vicariance is assumed to be the main cause of concordant phylogenetic patterns among co-distributed clades, and dispersal and extinction are invoked primarily to explain discordance among clades. However, dispersal, vicariance and extinction are all linked directly to ecological processes, and the likelihood that any of these processes explains a given pattern depends on ecological factors, such as dispersal ability and habitat fidelity. Little attempt has been made to bring ecological information to bear on cladistic biogeography.

New GIS-based methods for ecological niche modeling offer one approach for incorporating ecological information in cladistic biogeography. Given data describing the climatic conditions for locations where a species or clade exists today, an ecological niche model can be made to predict where a species or clade occurs, given its inferred environmental tolerances [44]. Assuming that these tolerances remain similar over time, and given some information about past climates in the biogeographical region in question, the distribution of acceptable habitats for the lineage can be projected back onto maps for different points in time [45]. Thus, it should be possible to predict pathways for dispersal between areas that are no longer connected by suitable habitat, and reveal areas that lacked sufficient suitable habitat at crucial points in the past (suggesting local extinction). Such analyses might also illuminate the relative timing of biogeographical connections and barriers.

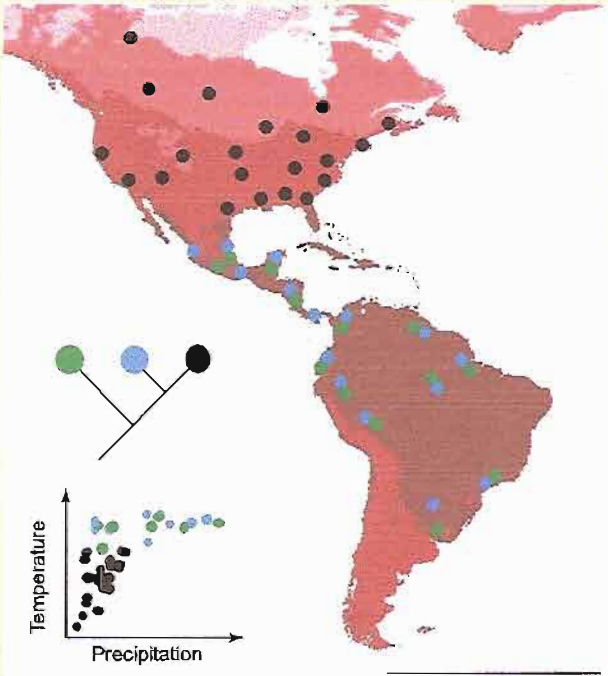
We think that even crude ecological information (e.g. about general climatic tolerances of taxa and past climates of regions) can offer invaluable insights into cladistic biogeography. For example, dispersal of some terrestrial groups between continents not only requires a terrestrial connection, but also suitable climate in the region of that connection during the time frame of the putative dispersal event [46].

Box 2. Phylogenetic niche conservatism and niche evolution

Phylogenetic niche conservatism [27,44,47,48] can be a crucial factor in explaining large-scale patterns of distribution. The fundamental niche of a species describes the abiotic conditions in which it can persist and maintain viable populations [49]. We specifically refer to the geographical range, rather than other aspects of the niche (e.g. diet). Although organisms collectively occupy a wide range of environmental conditions on Earth, most species and clades occupy only a limited subset of these. This set of acceptable conditions can be determined by intrinsic organismal traits, such as physiology, and can be maintained over long evolutionary timescales. For example, many groups of organisms are globally widespread in tropical regions, but have not successfully invaded or radiated in temperate regions, despite tens or hundreds of millions of years of opportunity (e.g. onychophorans, cycads and caecilians). If there is niche conservatism within a clade, then the ancestral niche can determine the regions and habitats to which the clade can spread, and those in which it will persist in the face of environmental change. Although niche conservatism can be seen as a pattern or outcome rather than a process, it can be actively maintained by microevolutionary forces over time [27].

Niche evolution (i.e. the expansion of niche breadth or specialization for new conditions) should enable invasion of new habitats and climatic regimes that had previously limited the distribution of a clade (Figure I). Even though certain niche characteristics might be shared by all members of a clade through phylogenetic descent, niche evolution can only occur in individual species. Thus, changes in niche breadth in one species in one part of the range of a clade might have only a limited impact on the overall distribution of the clade. We think that the interplay between niche conservatism and niche evolution will prove to be a major theme in the biogeographical history of many clades.

Evidence for niche conservatism can come from the repeated failure of a clade to invade habitats or climatic regimes that are adjacent to its geographical range at several independent points (Figure I), with each point potentially representing an independent replicate for statistical analysis. New GIS-based tools should also facilitate quantification and phylogenetic analysis of niche conservatism and niche evolution [44–45,50]. The strongest evidence for niche conservatism should come from dissecting the ecophysiological traits that underlie the geographical range limits of species and clades, and from determining the microevolutionary forces that limit evolution in those traits.



TRENDS in Ecology & Evolution

Figure I. Hypothetical example illustrating niche conservatism and niche evolution. Different colored dots on the map and graph indicate localities for members of three clades. Lighter shades of red indicate colder yearly minimum temperatures. Two of the clades (blue and green) exhibit niche conservatism. Species in these clades are confined to tropical climates and fail to invade cooler regions in North America, southern South America, and high elevations, despite their geographical proximity to these areas (we assume that their spread into these regions is not limited by competition). The third clade (black dots) exhibits niche evolution relative to the other two. This clade has invaded temperate regions (presumably by evolving tolerance to freezing winter temperatures) and no longer occurs in the ancestral tropical climatic regime.