Toward an Integrative Historical Biogeography[1]

Michael J. Donoghue[2] and Brian R. Moore

Department of Ecology and Evolutionary Biology, Yale University, P.O. Box 208106, New Haven, Connecticut 06511

Synopsis. Cladistic biogeographic methods remain susceptible to the confounding effects of "pseudo-congruence" and "pseudo-incongruence" because they were not designed to incorporate information on the absolute timing of the diversification of lineages. Consequently, results from cladistic biogeographic studies are difficult to interpret and cannot be confidently attributed to any particular cause. We illustrate these points with concrete examples, paying special attention to recent work on the biogeography of the Northern Hemisphere, and outline ways in which topological and temporal information might be better integrated. The development of historical biogeography over the last few decades provides general insights into the nature of integration through the life of a discipline.

Introduction

Despite its very promising beginnings, we agree with the assessment of Nelson and Ladiges (1996, p. 54) that cladistic biogeography has yielded few genuinely new insights over the last twenty years. When a research program is unproductive for a long period it suggests that something may be wrong with the questions being asked or the methods being used. Here we highlight several elements that have been missing from cladistic biogeographic approaches, focusing particularly on temporal information, and suggest how these might be integrated.

The value of incorporating temporal information in such studies has already been recognized (see references below). Our aim here is to help characterize and illustrate the problem using concrete examples from both the Southern and Northern Hemispheres. The Northern Hemisphere problem provides an especially good example of the difficulties faced by cladistic biogeographic methods, as well as insights into what can be gained by integrating time and directionality. Although we do not propose a new biogeographic method, we highlight several possibilities by comparison to methods recently developed to analyze the coevolution of hosts and their parasites.

Finally, in the spirit of the symposium that motivated this paper, we offer some general reflections on "integration." Specifically, recent developments in historical biogeography suggest to us that the degree of integration is something that changes in predictable ways through the ontogeny of a discipline, reflecting shifts in the perceived reliability of potentially relevant information.

The integration of phylogeny and biogeography

The fundamental idea underlying cladistic biogeography is that general patterns demand general explanations. Leon Croizat (*e.g.,* 1958, 1964) championed this outlook in seeking generalized "tracks" linking areas of endemism. Willi Hennig (1966) advanced the idea of overlaying phylogenetic trees on geographic maps to help determine former connections among areas and the direction of movement within lineages. Lars Brundin (*e.g.,* 1966) synthesized these two great ideas in his studies of midges in the Southern Hemisphere, searching for general phylogenetic patterns in the geographic distribution of multiple clades. Collectively, this work represented a significant departure from (and improvement upon) the previous practice of developing narrative biogeographic scenarios on a case-by-case basis.

In the hands of Donn Rosen, Gareth Nelson, and Norman Platnick these insights were subsequently refined and formalized (*e.g.,* Rosen, 1975, 1978; Platnick and Nelson, 1978; Nelson and Platnick, 1981; Nelson and Rosen, 1981). The goal of the resulting cladistic biogeographic program was to identify general patterns in the relationships among geographical areas of endemism, which would therefore suggest the need for general explanations such as vicariance caused by particular events in Earth history or concerted dispersal. In general, this approach entails the compilation of "taxon area cladograms" (phylogenies in which the names of terminal taxa have been replaced by the areas in which they occur) and the search for patterns of topological congruence expressed in the form of "general area cladograms."

It was evident immediately that in practice the search for topological congruence would be confronted by ambiguity associated with widespread taxa, redundant distributions, and missing taxa (*e.g.,* Nelson and Platnick, 1981; Page, 1990). This led to the development of several methods, especially "component analysis" (*e.g.,* Nelson and Platnick, 1981; Page, 1990, 1993a) and "Brooks parsimony analysis" (*e.g.,* Brooks, 1981, 1985, 1990). Component analysis searches for general area cladograms under a variety of *a priori* assumptions about the evidential significance of widespread species, etc. Brooks parsimony analysis renders individual taxon area cladograms as a matrix of binary characters and then combines these in a single parsimony analysis. In general, deviations from the emergent pattern of topological congruence

are attributed to lineage-specific processes, such as extinction and dispersal (*e.g.,* Brooks, 1990; Brooks and McLennan, 1991). The biogeographic problem is analogous to the inference of other types of historical associations, such as the coevolution of host-parasite systems and the "gene tree/species tree" problem, which have analogues to lineage-specific processes (*e.g.,* "dispersal" has been equated with "host switching" and "horizontal transfer": Page, 1993*b*, 1994; Maddison, 1995, 1997; Page and Charleston, 1998).

More recently there have been a variety of methodological developments. From component analysis emerged "reconciled tree analysis" (Page, 1993*b*, 1994), "three-item statements analysis" (Nelson and Platnick, 1981; Nelson and Ladiges, 1991*a, b*), and "paralogy-free subtree analysis" (Nelson and Ladiges, 1996; Ladiges, 1998). Brooks parsimony analysis has also been extended, especially in what has been called "secondary BPA" (*e.g.,* Brooks, 1990; Brooks and McLennan, 1991; Brooks *et al.*, 2001).

The details of these methods have been reviewed elsewhere (*e.g.,* Morrone and Carpenter, 1994; Morrone and Crisci, 1995; Humphries and Parenti, 1999). We mention them here to emphasize that while a number of methods have been developed, they are fundamentally similar with respect to the present arguments. Most importantly, they are "topology based," meaning that general patterns are sought by comparing or combining only the topologies of component taxon area cladograms. Although there has been discussion of the ages of lineages, especially in the context of explaining observed conflicts among area cladograms, cladistic biogeographic methods have not directly incorporated information on the absolute timing of diversification in the component lineages. They also do not directly incorporate inferences on the place of origin or the directions of migration within particular lineages.

What's Wrong With Excluding Temporal Information?

Briefly, knowledge of the timing of events distinguishes those groups that diversified during the same time period, and therefore might have experienced the same causal events, from those that diversified during different time periods and require different causal explanations (*e.g.,* Grande, 1985; Hafner and Nadler, 1990; Page, 1990, 1991, 1996; Cunningham and Collins, 1994; Hedges *et al.*, 1994; Huelsenbeck *et al.*, 1997; Xiang *et al.*, 1998; Voelker, 1999; Donoghue *et al.*, 2001; Hunn and Upchurch, 2001; Sanmartín *et al.*, 2001). Ignoring temporal information obscures the connection between biogeographic patterns and their underlying causes.

To see this point, imagine that two clades with endemic species in areas A, B, and C are included in a cladistic biogeographic analysis. Further suppose that one of the groups diversified in the Cretaceous and the other during the Miocene. What are the possible outcomes? One possibility is that topologies of the taxon area cladograms for the two groups agree, say, on
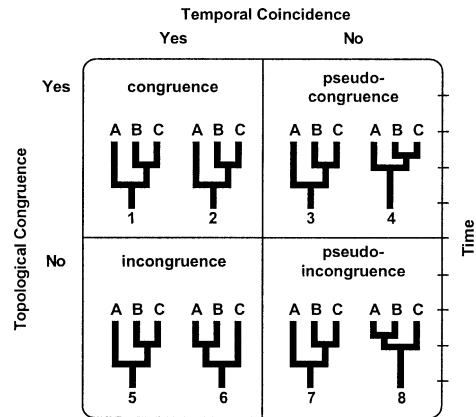

Fig. 1. The test of time in historical biogeography. Congruence and incongruence refer to clades that diversified synchronously and exhibit the same or different taxon area relationships, respectively. Pseudo-congruence and pseudo-incongruence refer to clades that diversified at different times, but exhibit the same or different taxon area relationships, respectively (see text for discussion).

A(B,C). This phenomenon (*e.g.,* Hafner and Nadler, 1990; Page, 1990, 1991; Hedges *et al.*, 1994) has been called "pseudo-congruence" (Cunningham and Collins, 1994). The same area relationships were obtained, but at different times, and presumably with different underlying causes.

The other possible finding is that the topologies of the area cladograms for the two groups are in conflict, say, A(B,C) *versus* (A,B)C. This phenomenon (Page, 1990, 1991) may be referred to as "pseudo-incongruence." The cladistic biogeographic interpretation would be that the two groups were subjected to the same geological events but somehow responded differently. However, knowledge of the ages of the groups indicates that they actually diversified in response to different events.

These concepts are illustrated in Figure 1. "Congruence" and "incongruence" apply to lineages that diversified during the same time period and might therefore have been subjected to the same biogeographic causes. Congruence suggests a common cause, whereas incongruence implies lineage-specific phenomena, such as dispersal and extinction. In contrast, "pseudo-congruence" and "pseudo-incongruence" refer to cases in which lineages are not temporally coincident. Under these circumstances one can only obtain false-positive results or false-negative results. To the extent that they are intended to pertain to underlying causes, cladistic biogeographic methods implicitly assume that all of the clades under consideration diversified contemporaneously. The inclusion of groups of different ages therefore confounds the interpretation of the results.

A surprising variety of opinion exists on the issue of including temporal information. At one end of the spectrum is denial of the potential pitfalls of excluding data on the ages of clades. Humphries and Parenti (1999), for example, maintain that it is a "principle" of cladistic biogeography that "[a]ll taxa, regardless of

their presumed age. . . are treated equally in deriving biogeographic patterns," and furthermore that "[a] general explanation for a pattern applies equally to all taxa supporting the pattern" (p. 120). They argue that considering the possibility of different ages and different causes violates a more fundamental principle:

> . . . [I]f we recognize a pattern, all taxa sharing the pattern came to occupy the same areas at the same time in response to the same geological events. If this is not true, then any other taxon sharing the pattern and represented by younger fossils would have to have formed the same distribution pattern at a later date. Parsimony precludes this conclusion. That is the nature of a pattern in cladistic biogeography. (p. 145)

Nelson and Platnick (1981, pp. 541–543) expressed a similar outlook in discussing the possibility that a taxon area cladogram for *Homo sapiens* might correspond with a general area cladogram reflecting ancient seafloor spreading. They argued that regardless of much younger age estimates for humans (which they dismissed as unreliable), this result would compel us to consider that humans responded to these same ancient events.

Most cladistic biogeographers have not been so explicit but have nevertheless implicitly assumed that correspondence to a general pattern implies that individual lineages existed at the same time. For example, Cracraft (2001) interpreted the Gondwanan distribution of several bird lineages as evidence that diversification in these groups predated the major geological vicariance events in the Cretaceous. These particular lineages may well be old enough, but in other cases the apparent correspondence of taxon area cladograms to a vicariant geographic pattern has been shown by independent age estimates to be too young to have been impacted by the geological events in question. Davis *et al.* (2002) showed, for example, that disjunct distributions between South America and Africa in six clades within the plant group Malpighiaceae all significantly postdate the separation of these continents.

Another possible response to pseudo-congruence and pseudo-incongruence is to defend the utility of general area cladograms, independent of when particular geographic patterns were attained. For example, the general area cladogram A(B,C) might be used to predict that the closest relative of a randomly sampled species present in area C would most likely be found in area B. This would effectively divorce cladistic biogeography from the inference of causal processes.

At least in hindsight, a number of methodological developments may have been motivated by the recognition that inclusion of groups of different ages will cause confusion. For example, we interpret the paralogy-free subtree approach (Nelson and Ladiges, 1996; Ladiges, 1998) in this light. Briefly, this method works its way from the tips of an area cladogram toward the root, pruning out subtrees that are free of area redundancy and setting these aside for subsequent analysis.

Apparently, the idea is to exclude redundant geographic patterns in more inclusive ("deeper") subtrees that would confound the analysis. Although this process eliminates some obvious cases of temporal incongruence, it may still assemble a set of subtrees of quite different ages. A subtree pruned from one branch of a large tree could be older or younger than a subtree pruned from another branch, not to mention a subtree obtained from another taxon area cladogram.

A SOUTHERN HEMISPHERE EXAMPLE

To emphasize the importance of temporal information we consider an example from the Southern Hemisphere. Linder and Crisp (1995) performed an excellent cladistic biogeographic analysis of *Nothofagus* and 12 other flowering-plant clades with endemic species on the southern Pacific land masses. Specifically, they used a tree reconciliation approach (implemented in COMPONENT; Page, 1993*a*), under two different assumptions about widespread species, and obtained a general area cladogram in which Australia and New Zealand were more closely related to one another than either was to South America: SA(AU,NZ). As they noted, this pattern conflicts with analyses of several insect groups and with geological evidence on the history of the land masses, which indicate a closer connection between South America and Australia: (SA,AU)NZ. According to standard interpretations, New Zealand has been isolated for some 80 million years (Myr), whereas Australia and South America were connected through Antarctica until *ca.* 40 million years ago (Mya).

In interpreting their results, Linder and Crisp (1995) briefly considered, but rejected as unlikely, the idea of concordant dispersal, noting however that this alternative hypothesis could be tested with temporal information. Specifically, they reasoned that dispersal from Australia to New Zealand would have occurred sporadically since the establishment of the westerly circulation *ca.* 30 Mya, which would predict that they achieved their current distributions at a number of different times. In the end, Linder and Crisp (1995) suggested that "the conventional chronology of continental breakup may not accurately reflect the establishment of disjunctions in the biota" (p. 20) and noted the possibility of more recent and more ancient land connections.

The point we wish to stress is that it is impossible in this analysis, as in all such cases, to understand the significance of the results with respect to underlying causes in the absence of information on the times at which the various taxa diversified. In Figure 2 we show a variety of possibilities, where phylogenies are embedded within the presumed history of the land masses. Figure 2A shows a group in which the ancestral species occupied the ancestral land mass and subsequently speciated in association with the sequential geological fragmentation of the areas. The resulting taxon area cladogram for this group is topologically and temporally consistent with the geological clado-
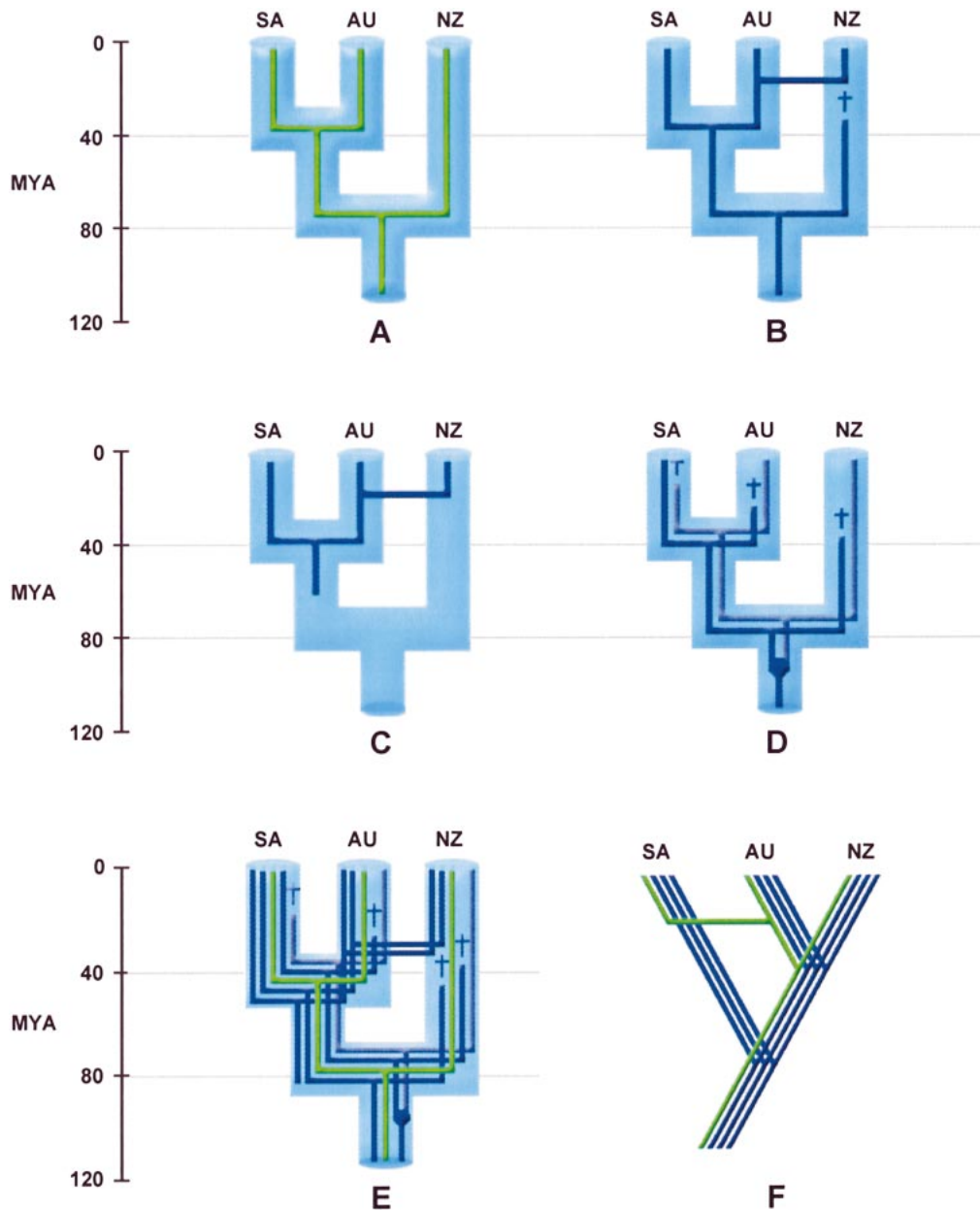
FIG. 2. Hypothetical example inspired by Linder and Crisp's (1995) analysis of Southern Hemisphere biogeography. The containing (tubular) trees represent the accepted geological history of the three areas: Australia (AU), South America (SA), and New Zealand (NZ). The contained trees represent taxon area cladograms for particular clades. In (A) the taxon area cladogram is temporally and topologically consistent with the geological sequence, whereas in (B), (C), and (D) the taxon area cladograms and geological sequences are variously inconsistent owing to dispersal and extinction (see text). (E) combines the information in (A), (B), (C), and (D), indicating several instances of extinction in NZ and subsequent re-colonization from AU. (F) illustrates the general area cladogram likely to result from a cladistic biogeographic analysis (see text for discussion).

gram. Figure 2B shows a case in which the common ancestor of the group was present in the ancestral area, and diversification generally paralleled the break up of the areas (as in Fig. 2A). However, extinction of the NZ endemic (perhaps associated with the submersion of the island during the Oligocene; *e.g.,* Cooper and Cooper, 1995), followed by re-colonization by a member of the AU lineage, results in conflict between the taxon area cladogram and the geological history.

Figure 2C, D show groups that are younger or older,

respectively, than the geological events. In Figure 2C the ancestor of the group was not present in the ancestral area. Perhaps it entered from outside the region sometime during the 40-Myr interval between the two geological splits. As in Figure 2B, the NZ species originated by dispersal from AU, such that the taxon area and geological cladograms are incongruent. Figure 2D shows a more complicated scenario. This involves an older group in which speciation occurred within the ancestral area before the first geological split (and

therefore was not caused by that vicariance event), resulting in two lineages in the ancestral area. Subsequent extinction of the SA endemic in one lineage, and of the AU and NZ endemics in the other lineage, creates a pattern analogous to ''lineage sorting'' in molecular evolution, such that the taxon area cladogram is again incongruent with the history of geological fragmentation.

These four scenarios are combined in Figure 2E, which suggests a history of increased extinction in NZ during the last 40 Myr, and of more recent re-colonization of NZ from nearby AU. Only one of the area cladograms in Figure 2A–D matches the geological history, while the other three support the same alternative, SA(AU,NZ). Under these circumstances, a simultaneous cladistic biogeographic analysis would yield the general area cladogram shown in Figure 2F, which happens to match the result obtained by Linder and Crisp (1995).

Several general conclusions may be drawn from this exercise. First, only groups that were present in the region and were exposed to the vicariance events in question can be expected to exhibit taxon area cladograms that match the geological history. Even in such cases, however, the correspondence may be imperfect owing to lineage-specific processes, such as extinction and dispersal (Fig. 2B). On the other hand, groups that diversified in the region, for example, well after the events in question (as in Fig. 2C) are not expected to be congruent with the geological history of vicariance events. Instead, such groups can only be pseudo-congruent or pseudo-incongruent. It follows that if we want to assess the impact of particular vicariance events, such as the fragmentation of Gondwana, we should choose groups of the appropriate age. Clearly, this requires an independent assessment of divergence times.

Second, the results of standard cladistic biogeographic analyses, which may combine groups of different ages, cannot be unambiguously attributed to any particular cause. Whether the results of Linder and Crisp (1995) indicate that the conventional geological interpretation is incorrect, or that extinction in NZ was followed by concerted dispersal from AU, depends critically on temporal information. If all, or even most, of the groups included in the analysis diversified in the appropriate time frame (for starters, if we knew that they were approximately 80 Myr old), then we would have reason to question the geological evidence. However, if the study groups diversified much more recently, say over the last 30 Myr, the analysis would simply not be relevant to testing the particular vicariance scenario in question.

NORTHERN HEMISPHERE BIOGEOGRAPHY

Cladistic biogeographers have paid more attention to the Southern Hemisphere than to the Northern Hemisphere, in part because the relatively simple geological and climatological history of Gondwana makes this a more tractable system. Connections among the
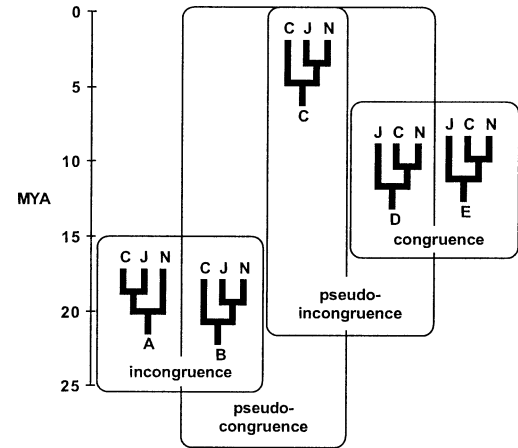

FIG. 3. Examples from Donoghue et al.'s (2001) analysis of Northern Hemisphere biogeography showing each of the possibilities depicted in Figure 1: A. *Torreya*, B. *Hamamelis*, C. *Weigela-Diervilla*, D. *Triosteum*, and E. *Buckleya* (see text for discussion).

major Laurasian geographic provinces have changed over time; for example, with the widening of the Atlantic and the intervention of intercontinental seaways. During the Tertiary, several major migration pathways facilitated biotic exchange between the Old World and New World, but shifting latitudes and climates rendered these paths more-or-less accessible to organisms with different physiological tolerances and dispersal capabilities (Sanmartín et al., 2001; Tiffney and Manchester, 2001). For example, thermophilic evergreen plants were able to move between Asia and North America across the so-called North Atlantic Land Bridge through the Eocene, but such movement was subsequently cut off. Migration across the Bering Land Bridge was intermittently feasible throughout the Tertiary, depending on sea-level and climatic conditions. In addition to these complexities, there have been differential extinction rates among regions. In particular, drying in western North America and cooling in Europe appear to have increased extinction rates in these areas relative to eastern Asia and eastern North America, where pockets of equable climate maintained greater diversity. More recently, of course, the Northern biota has been profoundly impacted by repeated episodes of glaciation.

Recently, a number of phylogenetic studies of Northern Hemisphere biogeography have been conducted that have explicitly incorporated age estimates for major disjunctions as well as inferences of ancestral areas and the direction of movement within lineages (e.g., Sanmartín et al., 2001; Xiang et al., 1998, 2000; Donoghue et al., 2001; Xiang and Soltis, 2001). To highlight the insights made possible by integrating such information, we focus here on examples from Donoghue et al. (2001). Their analysis centered on seven plant groups with intercontinental disjunctions and species distributed in three or more major areas of endemism. The placement of fossils provided calibration points for molecular dating in all but one of these
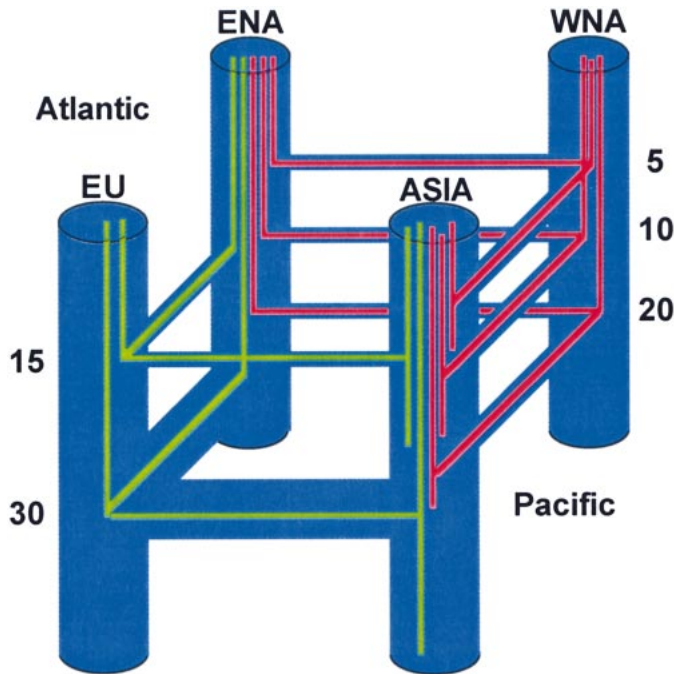
FIG. 4. A representation of the area cladograms, diversification times, and inferred patterns of movement for the taxa studied by Donoghue *et al.* (2001). Northern Hemisphere geographic regions are represented by vertical tubes; horizontal connections between these indicate inferred movement at different time periods (Recent at the top, numbers indicate millions of years before present). Note that these taxa are inferred to have moved in different directions around the Northern Hemisphere (through the North Atlantic in some cases, and through Beringia in others), and to have entered eastern North America at different times (see text for discussion).

cases (*Buckleya*, for which a substitution rate was obtained from the literature). Where a molecular clock was rejected, non-parametric rate smoothing was used to estimate divergence times (Sanderson, 1997), and standard errors on divergence dates were estimated using parametric bootstrapping (cf., Baldwin and Sanderson, 1998). Dispersal-vicariance analysis (implemented in DIVA; Ronquist, 1996, 1997*a*, *b*) was used to infer ancestral areas and the direction of migration in each clade. This method places one or more ancestral areas (depending upon the constraints imposed) at each internal node so as to minimize the costs associated with dispersal and extinction events (Ronquist, 1997*a*, *b*).

Donoghue *et al.* (2001) found that the five study clades with species in China, Japan, and eastern North America exhibited all three possible relationships among these areas: (1) (China [Japan, North America]) in *Hamamelis* and the *Weigela-Diervilla* clade; (2) (Japan [China, North America]) in *Triosteum* and *Buckleya*, and (North America [China, Japan]) in *Torreya*. As indicated in Figure 3, age estimates for the intercontinental disjunction vary considerably among the five clades and provide examples of each of the hypothetical possibilities depicted in Figure 1. *Triosteum* and *Buckleya* appear to be genuinely congruent, having attained the same area relationships in the same

time frame. In contrast, *Hamamelis* and *Torreya* appear to be truly incongruent, having attained conflicting area relationships during the same time frame. Comparison of *Hamamelis* with *Weigela-Diervilla* provides an instance of pseudo-congruence, with parallel area relationships having been attained at different times. Finally, the comparison of *Weigela-Diervilla* with either *Triosteum* or *Buckleya* represents an instance of pseudo-incongruence, with conflicting area relations realized at different times.

The two other clades studied by Donoghue *et al.* (2001) included species in eastern Asia, Europe, and North America, but not in Japan or western North America. In both cases the European species appeared to be most closely related to one or more North American species, and movement was inferred to have occurred through the North Atlantic. However, in one case (*Liquidambar*) the Europe-North America disjunction was dated at *ca.* 35 Mya and in the other (*Cercis*) at *ca.* 15 Mya, indicating another instance of pseudo-congruence.

Regarding the region of origin and movement of clades, in five of seven cases DIVA analyses (outgroups added, two areas allowed per internal node) indicated diversification within Asia preceding migration to North America. Results for the other two cases were equivocal.

Figure 4 simultaneously displays conclusions from Donoghue *et al.* (2001) on area relationships, timing, and directionality. Disjunctions between Asia and North America appear to have resulted from movement both through the North Atlantic and through Beringia. Within each of these tracks it appears that intercontinental disjunctions arose at different times, implying iterated episodes of dispersal and vicariance. In the case of the Beringian pattern, these results extend the findings for mammals from the Paleocene and Eocene (Beard, 1998), implying periods of interchange throughout the Tertiary.

Results similar to these have been obtained in all other recent studies of the Northern Hemisphere (*e.g.,* Xiang *et al.*, 1998, 2000; Sanmartín *et al.*, 2001; Xiang and Soltis, 2001). Most importantly, patterns of dispersal and vicariance appear to have been repeated at different times, resulting in multiple cases of pseudo-congruence and pseudo-incongruence. Under such circumstances standard cladistic biogeographic analyses, which include all taxa regardless of their ages, would yield confusing results and erroneous inferences about underlying causes. For example, in the absence of temporal data all disjunctions between Asia and Europe might be attributed to the Turgai Strait (a Late Cretaceous epi-continental seaway). Likewise, disjunctions between western and eastern North America might all be attributed to the Mid-Continental Seaway, which subsided toward the end of the Cretaceous. While the ages of some clades might support such interpretations, others, including virtually all of the plant groups that have been investigated, are too young to have been affected by these barriers. Instead, it appears that

these disjunctions came about at different times and in response to a variety of different factors. The same reasoning applies to the major intercontinental disjunctions. In general, the history of the Northern Hemisphere has featured the iteration of processes that have impacted the biota at different time intervals, such as the repeated opening and closing of Beringia and episodes of glaciation.

Only by adding temporal data and inferences on directionality is it possible to discern such iteration. Eventually it should be possible to infer the time at which each component of the biota underwent migration and/or experienced various vicariance events. And, considering the biota of any particular region, we might eventually determine the source and the time of entry of each species, which would then permit inferences on the nature and the consequences of species interactions within communities.

REFLECTIONS ON METHODS

Increasing awareness of the need to integrate temporal information has motivated the development of several promising methods. A variety of *ad hoc* approaches have been devised in the context of specific biogeographic studies. For example, Donoghue *et al.* (2001), recognizing the potential problem of mixing clades of different ages, began by dividing their study groups based on details of their geographic distributions (into an Atlantic track and a Pacific track), reasoning that this might eliminate at least some such problems. As noted above, however, this clearly failed to eliminate all cases of pseudo-congruence and pseudo-incongruence (Fig. 3). In the end they favored a more direct alternative, namely sorting clades into categories at the outset based directly on previously obtained age estimates. Such a procedure would in no way discard topological information. Instead, it aims to first parse taxa into sub-sets of comparable age that were potentially subjected to the same dispersal-vicariance events.

Sanmartín *et al.* (2001) subdivided their data sets into several time periods (delineated by particular geological events) and graphed the relationship between time period and inferred dispersal-vicariance connections among areas. In this way they were able to discern, for example, that movement through the North Atlantic was more common in the Early to Mid-Tertiary, whereas trans-Beringian distributions were rare in that time period and more common later.

The summary diagrams in Sanmartin *et al.* (2001), like the model presented in Figure 4, provide a means of synthesizing and visualizing complex relationships between area cladograms, time, and directions of movement, but they clearly are not methods for the simultaneous analysis of such data. However, in the literature on co-speciation in host-parasite systems we see the development of a number of analytical tools along these lines (Page, 1990, 1996; Huelsenbeck *et al.*, 1997, 2000*a*), which should, for the most part, be portable to the biogeographic problem (Page, 1993*b*; Maddison, 1995, 1997; Page and Charleston, 1998).

Page (1990, 1996) proposed a two-step, non-parametric test of co-speciation: the first stage involves testing for significant topological congruence between the associated clades using component analysis (Page, 1993*a*); the second stage tests the prediction that topologically congruent components diverged simultaneously. Huelsenbeck *et al.* (1997) proposed a parametric analog of Page's (1990, 1996) approach, implemented in a maximum likelihood framework. This approach similarly provides tests for topological and temporal correspondence between associated phylogenies using a series of likelihood ratio tests. First, the maximum likelihood estimate for a model in which the associated topologies are constrained to be identical is compared to a more general model in which the topologies are permitted to differ. Given significant topological congruence, a second test compares a model in which the speciation times for the associated clades are identical to a more general model in which the associated clades are permitted to speciate at different times.

Subsequently, Huelsenbeck *et al.* (2000*a*) developed a Bayesian implementation of their co-speciation analysis that incorporated a simple model of host switching by parasites among hosts (analogous to dispersal of species among areas), in which host-switching events are assumed to occur at a constant rate over the entire history of the association. This approach evaluates the posterior probability density of the various model parameters using Markov Chain Monte Carlo, providing estimates of both the number of host-switches and of the rate of host-switching. This approach is attractive in that it does not assume that the associated phylogenies (topologies and branch lengths) are known without error, as alternative phylogenies are sampled from the posterior probability in proportion to their probable accuracy.

Development of a Bayesian approach to the co-speciation problem provides a versatile, model-based framework that is nevertheless computationally efficient, and so should enable the elaboration and implementation of even more parameter-rich biogeographic models. Progress will require the development of models that relax the assumption of equi-probable dispersal through time, allowing the probability of dispersal to be conditioned on the relative proximity of geographic areas through time, etc. Biogeographic models will also need to allow the specification of lineage-specific probabilities for dispersal and extinction.

Although co-speciation in host-parasite systems is similar in many ways to the species-area relationship in biogeography, the correspondence is not exact. Some differences are a matter of degree, such as the level of fidelity in the historical association: different associations lie along a continuum, from relatively high (*e.g.,* between genes and species), to intermediate (host-parasite associations), to relatively low fidelity (species-area associations). Accordingly, dispersal may

be more frequent than host-switching, which in turn may be more frequent than horizontal gene transfer in most systems. Other differences are more fundamental: although species phylogenies may be predominantly divergent, relationships among geographic areas are more often reticulate, with repeating episodes of connection and disconnection. Additionally, temporal and topological congruence between host and parasite phylogenies is readily interpreted in terms of co-speciation, whereas temporal and topological congruence between taxon area cladograms may reflect either a shared history of vicariance or one of concerted dispersal. Distinguishing between these alternatives will require additional information, such as the timing of relevant geological events. Although it is not without its challenges, we are optimistic that developments along these lines will greatly improve our ability to meaningfully integrate temporal information into biogeographic analyses.

REFLECTIONS ON INTEGRATION

Recent developments in historical biogeography suggest what might be a general model for the development of integrative methods. Our proposition is that even when it is clear from the outset that a discipline depends on the integration of different sources of information (as is surely the case in biogeography), the development of truly integrative methods is likely to occur in stages. At any point, but especially early in the development of a discipline, there will be a variety of practical constraints and a wide variance in the availability and reliability of different, potentially relevant data sources. In the interest of making progress, methods are devised initially to incorporate the most reliable information, while deliberately or inadvertently setting other data types aside, at least temporarily. Subsequently, the development of methods that incorporate additional sources of information is likely to occur when two conditions are met. First, it must become obvious that existing methods are inadequate because they exclude a particular source of information. Second, the availability and reliability of those data must have improved sufficiently that it seems productive to try to integrate them.

The inception of cladistic biogeography represented such a transition. It was widely appreciated, at least by the 1960s, that the conduct of historical biogeography in the absence of solid phylogenetic information was doomed to failure. At the same time, owing to conceptual advances, the development of new tools, and access to new sources of evidence, confidence in the ability to reliably estimate phylogenetic relationships increased dramatically. The development of cladistic biogeographic methods was the natural outcome.

However, the development of a phylogeny-based biogeographic approach was influenced by several extenuating circumstances. First, at that point biogeographic methods based on other sources of information were poorly developed. That is, it was not a matter of integrating phylogenetic trees into existing methods, but rather the invention of new methods. Second, as noted already, estimates of the absolute ages of clades were widely mistrusted at that time (*e.g.,* Platnick and Nelson, 1978, p. 3). Finally, these developments occurred in the context of philosophical concerns regarding the independence of systematic biology and the explanatory power of biogeographic hypotheses (*i.e.,* their ability to be falsified by and to provide critical tests of hypotheses generated outside of the discipline). What resulted was the development of methods based exclusively on the topologies of phylogenetic trees and the area cladograms derived from them. In turn, these methodological developments subtly re-oriented the discipline, with the goals increasingly framed in terms of area relationships, while de-emphasizing directions of movement and the temporal sequence of biotic assembly. Consequently, cladistic biogeography became increasingly isolated from other sources of data, especially on ages and ancestral areas.

We view the present circumstances in parallel terms. It has become clear that cladistic biogeographic methods, focused exclusively on topological congruence, are inadequate, and that the principle omission is information on the absolute timing of diversification in different lineages. Fortunately, confidence in temporal information is rapidly increasing, owing especially to the development of methods that better integrate fossil and molecular data (*e.g.,* Sanderson, 1997, 2002; Rambaut and Bromham, 1998; Thorne *et al.*, 1998; Culter, 2000; Huelsenbeck *et al.*, 2000*b*; Kishino *et al.*, 2001; Aris-Brosou and Yang, 2002; Thorne and Kishino, 2002). This is not to say, of course, that unambiguous results will always be obtained using such methods (this certainly is not the case), or that the confidence intervals associated with such estimates will be tight enough to discriminate between alternative hypotheses. In some cases vicariance events may occur in sufficiently rapid succession as to exceed the resolving power of our temporal estimates. Such cases certainly do not justify ignoring temporal information altogether. In fact, the situation has improved to the extent that excluding divergence-time estimates now seems like ignoring highly relevant data. At this stage, truly integrative methods are likely to emerge, since cladistic biogeography has laid a very solid phylogeny-based framework, and there is absolutely no danger that temporal data will somehow displace the use of phylogenies.

We view the incorporation of temporal information as the first step in a process that will eventually see the integration of other obviously relevant information, especially on directions of movement and the relative vagility of organisms. As we have suggested, in general, the pace of such developments will depend on the level of dissatisfaction with methods that fail to integrate a particular data source as well as on the assessment of the reliability of such data. This highlights the need to focus special attention on the development of better methods to infer past migration and also to measure and compare vagility. We look forward to such

developments and to the insights that will surely follow.

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