

The resurrection of oceanic dispersal in historical biogeography

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Geographical distributions of terrestrial or freshwater taxa that are broken up by oceans can be explained by either oceanic dispersal or vicariance in the form of fragmentation of a previously contiguous landmass. The validation of plate-tectonics theory provided a global vicariance mechanism and, along with cladistic arguments for the primacy of vicariance, helped create a view of oceanic dispersal as a rare phenomenon and an explanation of last resort. Here, I describe recent work that suggests that the importance of oceanic dispersal has been strongly underestimated. In particular, molecular dating of lineage divergences favors oceanic dispersal over tectonic vicariance as an explanation for disjunct distributions in a wide variety of taxa, from frogs to beetles to baobab trees. Other evidence, such as substantial gene flow among island populations of *Anolis* lizards, also indicates unexpectedly high frequencies of oceanic dispersal. The resurrection of oceanic dispersal is the most striking aspect of a major shift in historical biogeography toward a more even balance between vicariance and dispersal explanations. This new view implies that biotas are more dynamic and have more recent origins than had been thought previously. A high frequency of dispersal also suggests that a fundamental methodological assumption of many biogeographical studies – that vicariance is *a priori* a more probable explanation than dispersal – needs to be re-evaluated and perhaps discarded.

Introduction

A classic problem in biogeography is to explain why particular terrestrial and freshwater taxa have geographical distributions that are broken up by oceans. Why are southern beeches (*Nothofagus* spp.) found in Australia, New Zealand, New Guinea and southern South America? Why are there iguanas on the Fiji Islands, whereas all their close relatives are in the New World?

From Darwin's time until the 1960s, the predominant answer for such questions was 'oceanic dispersal' [1]. Although successful long-distance colonization was rarely witnessed, plausible dispersal (see Glossary) mechanisms were easy to imagine: light plant seeds and spores could be transported through the air, larger seeds could be carried by ocean currents, animals such as crocodiles and monitor lizards could swim at least moderate distances, winged

animals could fly to distant landmasses, and most kinds of organisms could be carried on natural rafts [2]. Darwin [3] and others supported the plausibility of oceanic dispersal through experiments demonstrating the survival of organisms (mostly plant seeds) that had been left in seawater for weeks or months and through sightings of logs or mats of vegetation floating far out to sea. More significantly, proponents of oceanic dispersal argued that some islands had never been connected to other landmasses; thus, the ancestors of all native organisms on such islands must have arrived by overwater dispersal. The effective colonization of remote islands by oceanic dispersal suggested that examples such as the southern beeches, involving continents and/or less remote islands, could be explained by the same mechanism.

During the 1960s and 1970s, two developments ignited a revolution in historical biogeography that drastically reduced the perceived importance of oceanic dispersal [4]. The first was the validation of plate-tectonics theory, which provided vicariance explanations on a global scale.

Glossary

Area cladogram: a cladogram in which the taxa have been replaced by the areas in which they occur. From an area cladogram, various algorithms can be used to derive a resolved area cladogram in which a single area is associated with each terminal node and each area is represented only once. A resolved area cladogram is meant to reflect the history of biotic connections among areas for that group [7]. For example, if areas A and B are grouped together in a resolved area cladogram to the exclusion of area C, this implies that A and B had a more recent biotic connection to each other than either did to C. Area cladograms or resolved area cladograms for multiple monophyletic groups can be synthesized into a general area cladogram that is meant to reflect the history of biotic connections shared by the different taxa [7]. If the areas are landmasses separated by oceans, the above pattern in a resolved area cladogram or a general area cladogram typically would be taken to mean that areas A and B formed a contiguous landmass after the separation of these two areas from C. However, the pattern also is consistent with more recent oceanic dispersal between A and B than between these two and C. Dispersal could produce the same history of connections in different groups for various reasons (e.g. because of the distances among the areas or the pattern of ocean currents [8,11]).

Continental island: an island that previously was connected to a continent.

Disjunct distribution: a discontinuous distribution of a species or higher taxon. Here, breaks in distributions are typically oceans separating landmasses.

Dispersal: extension of the geographical range of a species by movement of one or more individuals. Here, dispersal refers to movement of terrestrial or freshwater organisms across an ocean barrier.

Historical biogeography: the study of how events and processes in the past (e.g. vicariance, dispersal, speciation, and extinction) have affected the geographical distributions of taxa.

Oceanic island: an island, typically volcanic or coralline, that has never been connected to a continent.

Vicariance: separation of the geographical range of a species into two or more parts through the development of a barrier (or barriers) to dispersal (e.g. the formation of an ocean through rifting).

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Distributions such as that of the southern beeches made perfect sense under plate tectonics: such taxa could have been widely distributed on the ancient continent of Gondwana and simply 'drifted' with the separating fragments of the continent. The second important development was the spread of cladistic thinking. Cladistics provided an objective method for reconstructing phylogenetic relationships and, thus, a means of evaluating whether different taxa show histories of connections among areas that are concordant with each other and with the hypothesized vicariance history.

The vicariance biogeography that emerged from the melding of plate tectonics and cladistics was appealing for several reasons. In particular, it provided unifying explanations for the disjunct distributions of many taxa. For example, the fragmentation of Gondwana could explain not only the distribution of southern beeches, but also that of other widely distributed groups, such as cichlid fishes, pleurodiran (side-necked) turtles, and ratite birds, among others [5]. In addition, vicariance hypotheses were clearly falsifiable: the importance of specific vicariance events for a particular taxon could be refuted if the branching history of the lineages did not match the hypothesized vicariance history. By contrast, cladistic biogeographers claimed that hypotheses of dispersal were not falsifiable because all patterns of relationships can be explained by some dispersal hypothesis [6]. Vicariance biogeographers often sounded positively contemptuous of a dispersalist biogeography; for example, Nelson [1] described dispersalism as 'a science of the improbable, the rare, the mysterious, and the miraculous.'

Whether by the inherent logic of the above arguments or by the stridency of its advocates, vicariance came to dominate historical biogeography [7]. Dispersal was conceded for oceanic islands, but, for cases that could be explained by either vicariance or dispersal, most biogeographers assumed that vicariance was the more probable explanation [4]. However, the pendulum is now swinging back. The past few years have seen a strong increase in the number of studies that support oceanic dispersal, often in cases that had been explained previously by vicariance. Collectively, these studies represent a major shift in historical biogeography that has profound implications both for how we view the geographical history of biotas and for the methods that we use to decipher that history.

Oceanic dispersal, not tectonic vicariance

The fit between area cladograms and hypothesized vicariance sequences (inferred from geological or other evidence independent of the area cladograms) often has been considered to be the primary evidence in favor of vicariance. For example, such evidence supposedly corroborates the hypothesis that Gondwanan fragmentation has had a dominant influence on the current distributions of Southern Hemisphere taxa (see references in [8]). However, over the past 20 years, many investigators have pointed out that vicariance hypotheses require that speciation and the corresponding fragmentation of areas must occur at the same time, and thus that information on the absolute timing of speciation events is crucial in evaluating such hypotheses (e.g. [9–12]).

The new support for oceanic dispersal has come primarily from information on the timing of speciation, fueled by the development of improved methods of DNA sequencing and of estimating lineage divergence dates based on molecular sequences. In a typical case, sister taxa occur on opposite sides of an ocean barrier and the competing explanations are a relatively old vicariance event and a more recent oceanic dispersal. In many such cases, the molecular divergence (e.g. in nucleotide or amino acid sequences) apparently is too small to be explained by vicariance. For example, Baum *et al.* [13] found that DNA sequences of the internal transcribed spacer region for baobab trees (*Adansonia* spp.) suggest a divergence age of 5–23 million years for taxa in Africa versus Australia. Even the oldest estimate is far too recent to be explained by the tectonic separation of these continents, which occurred ~120 million years ago [14]. Other taxa for which molecular dating has supported oceanic dispersal over tectonic vicariance include freshwater teleosts [15,16], carnivores [17], lemurs [17], monkeys [18], squamate reptiles [19,20], frogs [21], flightless insects [22], and angiosperms in the Malpighiaceae [23], Rapateaceae [24], and Atherospermataceae [25], among many others.

The fossil record also has been used to date lineage divergences and, thus, to evaluate competing vicariance and dispersal hypotheses. In particular, first appearances of taxa in the fossil record have been used to suggest that a divergence occurred too recently to be explained by vicariance. For example, Lundberg [10] argued from the first appearance of cichlids in the fossil record that this widespread Southern Hemisphere group had not yet evolved during the period of Gondwanan fragmentation. He noted that several increasingly higher-level taxa within which cichlids are nested also do not appear in the fossil record until after Gondwanan fragmentation, further strengthening his case. Briggs [26] reviewed similar arguments for aplocheiloid fishes, ratite birds, and parrots. Other recent examples include baobab trees [13], chameleons [19], and several groups of mammals [17,27]. The geographical distribution of taxa in the fossil record can also cast doubt on vicariance. For example, Pole [28] noted that most extant New Zealand angiosperm lineages are not known from the late Cretaceous of that region. Even if these taxa existed during the breakup of Gondwana, if they were not in New Zealand at the time, then they must have arrived later by oceanic dispersal.

The original evidence for vicariance – the fit between area cladograms and the history of fragmentation of areas and the agreement among area cladograms for different taxa – also might have been overstated. For example, in a broad analysis of Southern Hemisphere taxa, Sanmartín and Ronquist [8] found that only two of 11 plant taxa showed area cladograms that were congruent with Gondwanan fragmentation. Although such mismatches between area cladograms and tectonic fragmentation do not necessarily imply oceanic dispersal, in many such cases dispersal is the most plausible explanation because the prior existence of land connections (e.g. resulting from lowered sea levels) that could explain current distributions is unlikely [e.g. 19,29].

Box 1. Continental islands, mass extinctions, and oceanic dispersal

The biotas of continental islands, such as New Zealand and Madagascar, have often been viewed as relicts left over from the period when these islands were attached to continents. Although this view in its strict form is refuted by examples of oceanic dispersal to these islands, continental island biotas might still consist largely of relict lineages, with a sprinkling of more recent immigrants.

However, some recent studies suggest a radical departure from the idea of relict biotas for such islands. Pole [28,30] used the fossil record to argue that virtually the entire New Zealand flora derives from transoceanic immigration following the breakup of Gondwana. Studies using area cladograms and molecular dating analyses support this contention for many New Zealand plant taxa [29]. Similarly, molecular dating analyses have been used to argue that the vertebrates of the West Indies [11] and Madagascar [15] are derived mainly from transoceanic immigrants.

These claims of massive biotic turnover remain controversial (e.g. [46,47]), but, if true, they beg the question, 'Is there something unusual about continental islands?' One possibility is that taxa on such islands are more likely to go extinct than are their counterparts on continents simply as a function of smaller population sizes. A more intriguing notion is that continental islands are more likely to suffer

catastrophic extinction events than are continents. The idea here is that an event, such as a change in sea level, is more likely to kill all the individuals directly or eliminate all the habitat of many species on a continental island than it is on a larger continental landmass. Transoceanic immigrants might then be more likely to establish themselves in the resulting ecological 'vacuum.'

Such catastrophic events might explain biotic turnover on several continental islands. For example, Hedges [11] has suggested that the bolide impact at the Cretaceous-Tertiary boundary wiped out nearly all West Indian vertebrates. Similarly, for New Zealand, submergence of most of the landmass during the Oligocene and/or rapid cooling during the late Miocene might have eliminated much of the Gondwanan flora [28,30]. The Chatham Islands, located some 800 km east of New Zealand, present an especially convincing case. These islands are geologically Gondwanan in origin, but are thought to have been entirely submerged in the Oligocene [28]. The taxa of the Chatham Islands differ very little from their relatives in New Zealand and must have arrived on the islands by recent oceanic dispersal [22]. These cases suggest that mass extinction causes the biotas of continental islands to converge on those of oceanic islands in being derived primarily from transoceanic immigrants.

Although the studies cited above represent many apparent cases of oceanic dispersal, it could still be that the great majority of disjunct distributions involving continents and continental islands result from tectonic vicariance. However, the results of some studies suggest that the overall role of oceanic dispersal for such continental landmasses is considerable. For example, molecular dating analyses [29] and lack of fit between area cladograms and the sequence of Gondwanan fragmentation [8,29] both indicate a major role for oceanic dispersal of plants to and from Australia and New Zealand. Pole [28,30] has gone even further, arguing from fossil evidence that almost the entire New Zealand flora derives from oceanic dispersal (Box 1).

Sanmartín and Ronquist [8] found less of a role for oceanic dispersal in Southern Hemisphere animals, consistent with the notion that animals have more difficulty in crossing ocean barriers than do plants. However, Hedges [11] and Vences *et al.* [15] used molecular dating analyses to suggest that most vertebrate species of the West Indies and Madagascar, respectively, are descended from transoceanic immigrants (Box 1).

It would be premature to conclude that dispersal is more important than vicariance in explaining distributions broken up by oceans. However, the above studies suggest that oceanic dispersal has played a significant role in generating such disjunct distributions for both plants and animals.

Problems with the evidence for dispersal over vicariance

A main objection to dispersal hypotheses is that they are unfalsifiable and thus unscientific (e.g. [6]). However, this can be countered by noting that, if plausible vicariance hypotheses are falsified, then dispersal is supported by default. In addition, specific dispersal hypotheses make predictions about the divergence dates and locations of sister lineages and, thus, are subject to refutation.

More compelling objections concern the quality or relevance of the fossil and molecular evidence used to refute vicariance. One can argue that the fossil record only

establishes minimum ages for taxa and, therefore, cannot show that a taxon is too young to have been affected by a vicariance event [31]. This argument is reasonable for taxa with poor fossil records. However, in other cases, the objection assumes a degree of incompleteness of the fossil record that strains credibility. For example, the Gondwanan vicariance hypothesis for cichlids requires origins during or before the early Cretaceous for several lineages that have abundant fossil records but that only appear in much more recent strata [10].

Molecular dating analyses have been criticized for a variety of reasons, including calibrations using suspect fossil dates, violation of the molecular clock assumption, absence of confidence intervals, and use of inappropriate taxa [32]. Some of the studies supporting oceanic dispersal suffer from one or more of these problems. However, at least some molecular dating studies (e.g. [17,20]) address these issues and most of them include conservative (i.e. relatively old) divergence estimates.

A more fundamental criticism is that fossil or molecular divergence dating methods are excessively inductive. For example, all molecular dating analyses must make assumptions about the rate of evolution of the lineages in question based on observations of other lineages. However, the sensitivity of results to different estimation methods, datasets, and calibration dates can be evaluated [33,34] and, as indicated above, conservative choices can be made in such analyses. Thus, the choice before us is between using induction carefully and conservatively or relying entirely on an area cladogram approach that ignores any information on the timing of lineage divergences.

Other striking examples of oceanic dispersal

Even in cases where oceanic dispersal was known or suspected, it might occur with higher frequency or across greater distances than expected. Here, I describe three such examples. (Box 2 concerns the related phenomenon of oceanic dispersal by taxa thought to be especially unlikely to disperse across saltwater.)

Box 2. Rafting frogs and torpid lemurs

'Batrachians (frogs, toads, newts)', Darwin noted in *The Origin of Species* [3], 'have never been found on any of the many islands with which the great oceans are studded.' He explained this absence by the fact that amphibians are quickly killed by seawater and are thus unlikely to cross oceans successfully. No biogeographer doubts that amphibians and certain other organisms (e.g. most terrestrial mammals, flightless birds) are especially poor oceanic dispersers. However, some recent studies show that it is unsafe to assume that such organisms never colonize new areas by crossing ocean barriers.

A striking example concerns two mantellid frog species found on Mayotte, an island of the Comoros archipelago some 300 km west of Madagascar [21]. The two species had been described as conspecific with taxa on Madagascar (where nearly all other mantellids are found) and were assumed to have been introduced. However, morphology and DNA sequences indicate that the two Mayotte taxa are distinct new species and, therefore, are natural endemics. The Comoros are volcanic and have never been attached to other landmasses; thus, the results strongly imply origins by natural, overwater dispersal.

Furthermore, the two species are not closely related within the Mantellidae, indicating two independent dispersal events.

Another case involves the carnivores and lemurs of Madagascar, medium-sized mammals that are considered poor oceanic dispersers. Yoder *et al.* [17] found through molecular dating analyses that both groups diverged from African mainland relatives long after the separation of Madagascar from Africa. The estimated divergence dates also do not match the hypothesized existence of a Cenozoic land bridge between Africa and Madagascar. Thus, both groups seem to have reached Madagascar by oceanic dispersal, perhaps facilitated by the ability to go into torpor.

Other examples of unexpected oceanic dispersal include monkeys from Africa to South America [18], flightless insects from New Zealand to the Chatham Islands [22], multiple dispersals by chameleons in the Indian Ocean [19], several other amphibian cases [21], and, more controversially, flightless ratite birds to New Zealand [26]. Although Darwin apparently was wrong in thinking that amphibians never cross saltwater, these cases reinforce a general message of the great evolutionist: given enough time, many things that seem unlikely can happen.

Plants of Tasmania and New Zealand

Tasmania and New Zealand are separated by 1500 km of ocean, yet share some 200 native plant species (excluding orchids) that presumably all dispersed over the Tasman Sea. The 200 species represent 15.2% of the Tasmanian flora and 12.6% of the New Zealand flora [35]. If we assume that these species persist for an average of 4–5 million years [35], most of them must have dispersed between Tasmania and New Zealand during the past few million years.

Recent dispersal to the Hawaiian Islands

Although the oldest current main island of the Hawaiian archipelago (Kauai) is only five million years old [36], now-submerged islands in the chain date back ~32 million years [37]. This has led to the notion that much of the current biota is derived from short-distance dispersal from these older islands [37]. Some Hawaiian radiations do seem to be older than the current islands (see references in [36]). However, Price and Clague [36] used geological modelling to claim that, at the time of the formation of Kauai, the archipelago consisted of relatively small and widely separated islands. They argued that this configuration would have drastically reduced colonization of Kauai and more recent islands from within the archipelago, which suggests that most of the current biota arrived from distant sources after the formation of Kauai. In a survey of molecular divergence date studies, they found that 12 of 15 Hawaiian radiations had most recent common ancestors estimated to be younger than Kauai, which is at least consistent with recent, long-distance origins.

Gene flow among *Anolis* lizards in the Bahamas

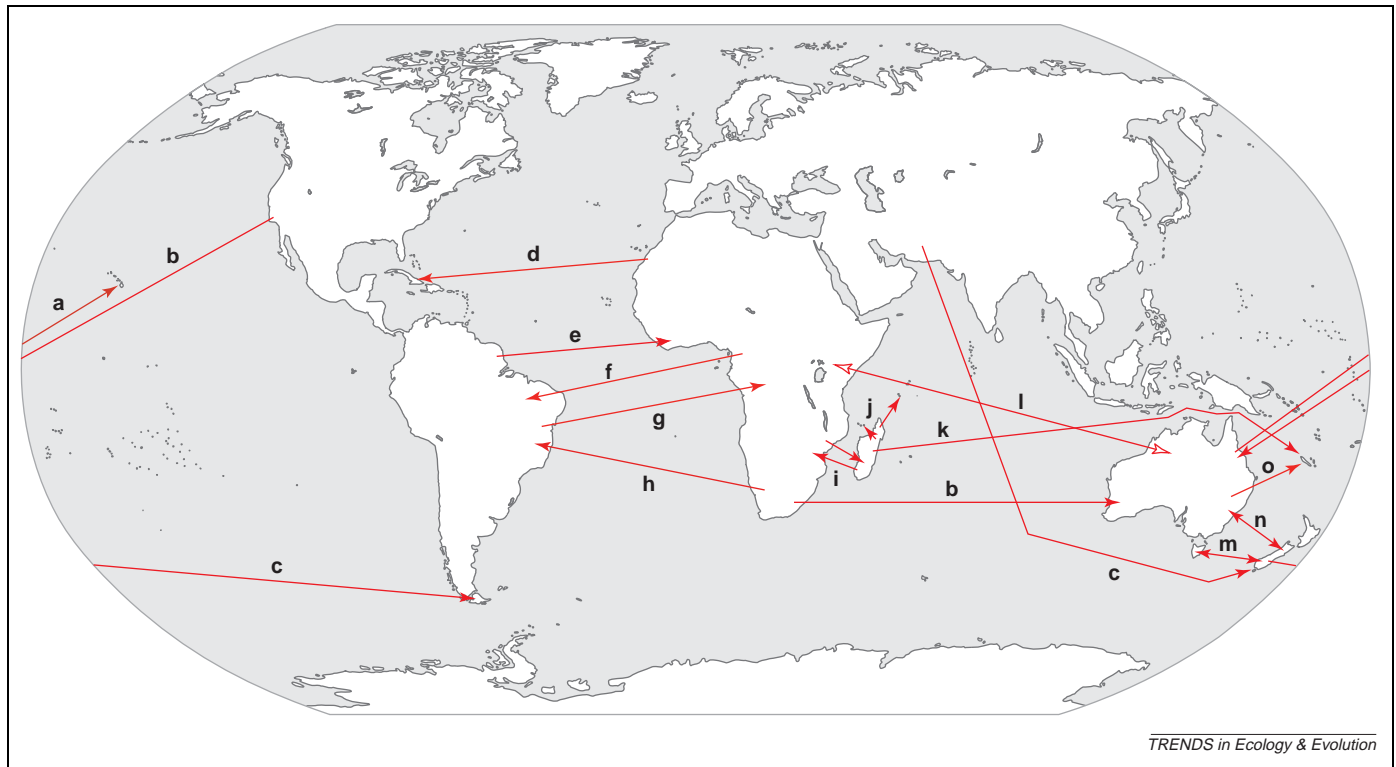
Using microsatellite data, Calsbeek and Smith [38] found considerable gene flow among islands for *Anolis sagrei* in the Bahamas (3.66 to 19.65 migrants per generation depending on the island pair). The direction of dispersal matched ocean current direction for all seven inter-island comparisons, thus implicating natural dispersal by rafting. Some of these islands are >100 km apart; thus, the frequency of oceanic dispersal is surprisingly high.

Along with the many studies favoring oceanic dispersal over vicariance and examples of dispersal of organisms thought to be especially bad dispersers (Box 2), the above three cases suggest that biogeographers have generally underestimated the frequency and importance of oceanic dispersal.

Implications

If vicariance biogeography was a revolution, we are now in the midst of a counterrevolution, driven primarily by new evidence in favor of oceanic dispersal [11,15,16,26,28,29,39,40]. Similar to the revolution before it, the counterrevolution represents a shift in perception about both the history of lineages and the methods for deciphering that history. As with so many issues in biology, the shift in perceived history concerns the relative frequency of different processes, from a view of vicariance as the dominant process in generating disjunct distributions to one involving a more even balance between vicariance and dispersal.

With respect to methodology, molecular dating and fossil evidence on divergence times have become crucial; as noted above, cases that are consistent with vicariance from a cladogram-matching perspective often favor dispersal when evidence on timing is considered. An important recent development is the synthesis of cladogram-matching and divergence times to infer general patterns from analyses of multiple groups (reviewed in [41]). However, even studies that use timing usually assume, either explicitly or implicitly, that a pattern consistent with either vicariance or dispersal is best explained by vicariance. If dispersal is as probable as some studies suggest, then this assumption might be inappropriate: even patterns consistent with vicariance sometimes might be better explained by dispersal. If this probabilistic reasoning is correct, then the future of historical biogeography might lie with methods that do not require an *a priori* preference for vicariance. Ronquist's [42] DIVA (dispersal-vicariance analysis) is one such method. DIVA places weights on vicariance and dispersal events to help infer the occurrence of these events. Although studies



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Figure 1. Striking examples of oceanic dispersal. **(a)** *Scaevola* (Angiospermae: Goodeniaceae) three times from Australia to Hawaii [48]; **(b)** *Lepidium* mustards (Angiospermae: Brassicaceae) from North America and Africa to Australia [49]; **(c)** *Myosotis* forget-me-nots (Angiospermae: Boraginaceae) from Eurasia to New Zealand and from New Zealand to South America [29]; **(d)** *Tarentola* geckos from Africa to Cuba [50]; **(e)** *Maschalocephalus* (Angiospermae: Rapateaceae) from South America to Africa [24]; **(f)** monkeys (Platyrrhini) from Africa to South America [18]; **(g)** melastomes (Angiospermae: Melastomataceae) from South America to Africa [40]; **(h)** cotton (Angiospermae: Malvaceae: *Gossypium*) from Africa to South America [51]; **(i)** chameleons three times from Madagascar to Africa [19]; **(j)** several frog genera to and from Madagascar [21]; **(k)** *Acridocarpus* (Angiospermae: Malpighiaceae) from Madagascar to New Caledonia [23]; **(l)** Baobab trees (Angiospermae: Bombacaceae: *Adansonia*) between Africa and Australia [13]; **(m)** 200 plant species between Tasmania and New Zealand [35]; **(n)** many plant taxa between Australia and New Zealand [8,28,29]; and **(o)** *Nemuaron* (Angiospermae: Atherospermataceae) from Australia (or Antarctica) to New Caledonia [25]. Unfilled arrows on both ends of a line indicate uncertain direction of dispersal. Filled arrows on both ends indicate dispersal in both directions.

using DIVA to date have assumed that dispersal is less probable than vicariance (e.g. [8]), the weights can be changed to reflect a higher probability for dispersal. Similarly, Huelsenbeck *et al.*'s [43] Bayesian method for analyzing host-parasite associations, if applied to studies of vicariance and dispersal, is not constrained to make vicariance more probable than dispersal. In short, the 'new biogeography' might involve not only reliance on the timing of lineage divergences, but also rejection of the fundamental assumption that vicariance is *a priori* the most probable explanation for disjunct distributions.

In the context of vicariance studies, dispersal typically has been viewed as a random process. However, the new emphasis on dispersal is rekindling interest in non-random aspects of the phenomenon. For example, some recent studies have emphasized factors, such as prevailing winds and ocean currents, that bias the direction of dispersal [8,11,44,45]. As knowledge of these abiotic factors increases, the sophistication of such studies of biased dispersal should also increase. In addition, there is renewed interest in organismal traits that influence dispersal ability. For example, the large number of plant species that have dispersed between Tasmania and New Zealand allowed Jordan [35] to correlate dispersal probability with specific reproductive and ecological characteristics.

A high frequency of oceanic dispersal also carries with it a profound implication for the timing of the

assembly of modern biotas. Specifically, it implies that the collections of lineages on particular landmasses are more recently derived than most biogeographers had believed. This is most strikingly the case for certain islands, such as New Zealand, Madagascar, the Chatham Islands, and perhaps the West Indies and Hawaiian Islands. However, it might also hold for continents (Figure 1) and include some cases in which substantial radiations have occurred in the newly colonized area. For example, chameleons apparently dispersed from Madagascar to Africa three times during the Cenozoic, giving rise to some 90 extant African species [19].

In the past few decades, biologists have increasingly recognized the rapidity of biotic change, as evidenced by studies of speciation, mass extinction, evolution within populations, and distributional shifts within landmasses. The new support for widespread oceanic dispersal adds to this dynamic view of life on Earth. Disjunct distributions must, to some extent, be explained by the slow drift of tectonic plates. However, increasingly it appears that this pattern is overlaid and obscured by something resembling an airline map (Figure 1) tracing the rafting, swimming, floating, and flying routes of countless transoceanic voyagers.

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