ESSAY

# Vagility: The Neglected Component in Historical Biogeography

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**Abstract** The conceptual gap between ecological and historical biogeography is wide, although both disciplines are concerned with explaining how distributions have been shaped. A central aim of modern historical biogeography is to use a phylogenetic framework to reconstruct the geographic history of a group in terms of dispersals and vicariant events, and a number of analytical methods have been developed to do so. To date the most popular analytical methods in historical biogeography have been parsimony-based. Such methods can be classified into two groups based on the assumptions used. The first group assumes that vicariance between two areas creates common patterns of disjunct distributions across several taxa whereas dispersals and extinctions generate clade specific patterns. The second group of methods assumes that passive vicariance and within-area speciation have a higher probability of occurrence than active dispersal events and extinction. Typically, none of these methods takes into account the ecology of the taxa in question. I discuss why these methods can be potentially misleading if the ecology of the taxon is ignored. In particular, the vagility or dispersal ability of taxa plays a pivotal role in shaping the distributions and modes of speciation. I argue that the vagility of taxa should be explicitly incorporated in biogeographic analyses. Likelihood-based methods with models in which more realistic probabilities of dispersal and modes of speciation can be specified are arguably the way ahead. Although objective quantification will pose a challenge, the complete ignorance of this vital aspect, as has been done in many historical biogeographic analyses, can be dangerous. I use worked examples to show a simple way of utilizing such information, but better methods need to be developed to more effectively use ecological knowledge in historical biogeography.

**Keywords** DIVA · Vicariance · Dispersal · Area cladogram · Vagility · Historical biogeography

## Background

Despite being the two arms of biogeography, ecological and historical biogeography are separated by a conceptual gap (Wiens and Donoghue 2004). Ecological biogeography seeks to understand the various factors, both biotic and abiotic, that affect the extant distributions of taxa while modern historical biogeography relies on phylogenetic relationships among taxa to answer the question of how geographic ranges of a particular taxon have evolved among a set of areas (Cox and Moore 2005; Lomolino et al. 2006). The two disciplines have much to offer each other (Lieberman 2003) since both are concerned with how extant distributional patterns arise. Yet, integration between them has been minimal, especially in the last few decades.

Distributions of a taxon evolve through three major processes: range-expansions, extinctions and allopatric speciation (Futuyma 1998). Allopatric speciation can be due to vicariance, where the range of an ancestral species is divided into two by a geographical barrier and the two populations on either side of the barrier diverge into two new species; speciation by vicariance (Mayr 1942). It can also be due to an ancestral species colonizing a new area across a pre-existing barrier and later diverging into two

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new species on either side of the barrier; speciation by dispersal (Platnick and Nelson 1978). Historically, dispersal and vicariance have been viewed as competing processes, with a strong debate about their relative importance (Zink et al. 2000; Brooks et al. 2001; Kodandaramaiah and Wahlberg 2007). However, the current view is more balanced and recognizes the importance of both processes (de Queiroz 2005). One of the aims of modern historical biogeography is to identify the processes such as vicariance, dispersal and extinctions at different points in the history of a given taxon (Crisci 2001; Wiens and Donoghue 2004) and a number of analytical methods to do so have been developed.

Most currently used phylogeny based inference methods are based on the principle of parsimony (Ree and Smith 2008; Sanmartín et al. 2008). Parsimony-based methods are based on straightforward assumptions and analyze distributional data within a strict parsimony framework relying on the generality of the assumptions made. It was long realized that vicariant events lead to common patterns across co-occurring taxa (Nelson 1969; Rosen 1978), whereas within-area speciation, extinctions and dispersals led to clade specific patterns. This has been exploited by biogeographers in a suite of analytical methods (Nelson 1969; Rosen 1978; Nelson and Platnick 1981; Zandee and Roos 1987; Page 1988; Brooks 1990; Nelson and Ladiges 1991; Page 1993; Wojcicki and Brooks 2005). Distributional data from multiple clades are analyzed together to detect common patterns, which are assumed to be caused by vicariance (Van Veller et al. 1999; van Veller et al. 2002). These are depicted as a 'General-Area-Cladogram' (GAC). Unique patterns for each clade are explained by dispersals, extinctions and within-area speciation events. Readers are referred to other works that describe differences between the various GAC-based methods (e.g., Morrone and Crisci 1995; Crisci 2001; van Veller et al. 2002; van Veller et al. 2003; Posadasa et al. 2006).

A second group of parsimony methods, event-based methods, use *a priori* assumptions about the probability of different processes and analyze individual taxa under these assumptions. Chief among these is Dispersal-Vicariance analysis (Ronquist 1997) implemented in the program DIVA (Ronquist 1996). This method has been the most widely used analytical method to infer vicariance and dispersal (323 citations since it was published; source ISI Web of Knowledge 2009). It assumes that vicariance and within-area speciation events are more likely to occur than dispersals and extinctions. Each of these four events is specified a cost that is inversely related to the assumed likelihood (Sanmartín et al. 2008). As currently implemented in DIVA, vicariance and within-area speciation are assigned a cost of zero, while dispersal and extinction are specified a cost of one. All possible reconstructions of

ancestral distribution states over the nodes are evaluated and the reconstruction with the least cost is considered the most parsimonious. The biogeographic history of the taxon is inferred using this reconstruction.

So far, all parsimony methods have largely ignored one aspect which has a big impact on the evolution of geographic ranges over time—the vagility or intrinsic dispersal ability of a species. It has been shown that ecological traits determining the vagility potential of species can affect their distributions (e.g., Doyen and Tschinkel 1974; Lomolino 1983; Shine 1987; Trejo-Torres and Ackerman 2001). Here I use a scenario of two islands to describe possible modes of evolution of geographic ranges and discuss the central role of vagility. Consider a scenario where two islands are separated by an oceanic barrier that disappears and reappears (for instance due to sea level changes in the Pleistocene). Frequency of colonization between any two islands by any species is proportional to its vagility. Let there be three ancestral species with differing vagility on one of the islands. Species 'H' has high vagility and can colonize one island from the other frequently and maintain geneflow across the barrier. Species 'L' has low vagility and can never do so, whereas species 'M' has moderate vagility and can colonize rarely.

The possible modes of geographic range evolution are:

A   *Vicariance Mode*: The barrier disappears and reappears. Disappearance of the oceanic barrier leads to range expansion of the species into the second island for all three species. This is followed by vicariance when the barrier reappears. Probability of this mode is highest in species L, followed by M. Species H has the lowest probability since frequent geneflow does not allow speciation.

B   *Dispersal Mode*: The barrier remains in place. Speciation occurs only when the species can colonize the second island rarely, because regular geneflow prevents speciation. Probability is highest in species M followed by H. L has near-zero probability.

C   *Widespread Species Mode 1*: The barrier remains in place. If initial colonization of the new island is followed by frequent genetic exchange between the two islands, this results in a widespread species even if the barrier is always present. Probability is highest in species H, followed by M. L has zero probability.

D   *Widespread Species Mode 2*: The barrier disappears and does not reappear. The species expands its range following disappearance of barriers as in Vicariance Mode. However, if vicariant barriers do not reappear, this results in a widespread species. Probability is equal among all species.

Within-area speciation can be ignored here in as much as it does not create new patterns of distribution. The

formation of widespread species (modes C and D) is not inherently a mode of speciation, but is an integral part in the evolution of distributions. Moreover vicariance can only act on widespread species, and even in case of speciation by dispersal the ancestral species is widespread during the period between dispersal and divergence.

In the examples above, the vagility of the taxon plays a significant role in determining the mode of evolution. As vagility increases the probability of Widespread Species Mode 1 > Dispersal Mode > Vicariance Mode = Widespread Species Mode 2. The strength of the barrier (distance between islands in this case), although quite relevant, is relative and intrinsically linked to vagility. Since all allopatric speciation events involve two areas with an intervening barrier, this island model can be extrapolated to allopatric speciation in general.

## Implications for Analytical Methods

I would first like to emphasize that the simplistic scenario of two islands used here always results in congruent patterns among two clades, be it dispersal or vicariance. In more complex scenarios, vicariance is more likely to lead to concordant patterns compared to dispersal. Nevertheless, in many instances, such as in this example, the two modes A and B generate the same patterns of distribution of the newly formed species. In this case, inferences from GAC-based methods are biased towards concluding that any common pattern is due to vicariance. Some attention has recently been paid to detecting common patterns resulting from multiple occurrences of Mode B, i.e., concerted dispersals or 'geo-dispersals' (Lieberman 2000; Lieberman 2003; Cook and Crisp 2005a; Halas et al. 2005; Folinsbee and Brooks 2007). However, congruence between two taxa with differing vagility can be the result of Mode A in one and Mode B in another. Thus, even perfect congruence is not strong evidence for vicariance when there is an ecological difference between taxa. I therefore argue that we can increase confidence in inferences of vicariance when taxa that are known to have similar ecology and life-history traits are analyzed together using a GAC-based method. Divergence time estimates in relation to geological events of course corroborate and strengthen inferences of vicariance.

The problem of ignoring vagility has more serious consequences for methods such as DIVA that attempt to infer historical processes based on information from a single clade. Here, all four modes are assigned the same cost, ignoring their relative probability of occurrence for each species. More importantly, all taxa are assumed to have the same dispersal probabilities between any two areas at all times. It is unreasonable to assume, for instance, that amphibians, that are well-known for their intolerance to

salinity, have the same probability of colonizing Madagascar from Africa as a migratory bird. Dispersal-Vicariance analysis can be realistic only if the relative costs assigned are realistic. The costs currently used in DIVA are rather arbitrary. de Queiroz (2005) has suggested that the cost of dispersal relative to vicariance should be changed to reflect the increasing acceptance of dispersal as a driver of speciation. However, different taxa will have different probabilities for any particular mode of speciation. Ideally, costs should be set based on the knowledge of the ecology of the organism and expectations about the relative probabilities of the different modes of range evolution.

Likelihood-based methods are relatively new and have not been used in many studies thus far. They are based on a parameterized model and can take into account multiple factors that might have affected historical distributions (Clark et al. 2008). The approach used by Ree and colleagues (Ree et al. 2005; Ree and Smith 2008) utilizes a complex model where the different events—dispersal, vicariance, within-area speciation and extinctions—are incorporated as parameters in a model. They call this the Dispersal-Extinction-Cladogenesis (DEC) model. Unlike DIVA, which assigns fixed costs (and hence probability) for the different events at all points in time, the composite model in this method can integrate information about lineage divergence times and the geological scenario to assign probabilities for different events. The probability of dispersal between specific areas at different points in time is parameterized in the form of a function describing the relative probability of dispersal success through time. This function can include relevant information about vagility. The range inheritance scenario with the highest likelihood is chosen as the best reconstruction. When analyzing individual clades, such holistic methods are the probably the way forward, especially with the availability of robust molecular phylogenies and the growing body of knowledge on the geological history of the earth (Riddle et al. 2008).

## Example 1

Von Bocxlaer et al. (2006) used DIVA to analyze distributions of two frog groups, Natatanura and Microhylidae. They inferred several vicariance events that were too young to be attributed to the break-up of Gondwanan fragments. For instance, putative vicariance events between India and Madagascar were inferred at the KT boundary (Cretaceous-Tertiary boundary; 65 mya or million years ago). Geological evidence points to the separation of India and Madagascar no later than 85 mya (Briggs 2003; Ali and Aitchison 2008). Similarly, vicariance events were inferred between Australia-New Guinea and Indo-Madagascar, and South America and Indo-Madagascar. Again, these were too young to be

congruent with the accepted timing of geological rifting (Von Bocxlaer et al. 2006). Amphibians are well-known to be intolerant to saline water and oceans are as a rule thought to be insurmountable barriers (Bossuyt and Milinkovitch 2001; Brown and Guttman 2002). Hence Von Bocxlaer and colleagues ruled out post-Gondwanan transoceanic dispersals to explain these patterns and instead argued that land connections between these landmasses existed for longer than previously thought, resulting in vicariance when the landmasses finally separated. They also invoked extinctions during the KT boundary. Their conclusions of Gondwanan vicariance are probably justified because there is no evidence that amphibians have dispersed naturally to oceanic islands (but see Vences et al. 2003; Evans et al. 2003).

Consider a situation where we had the same distributions and timing estimates for a group of butterflies. Being flying insects, butterflies are able to disperse longer distances and across marine barriers. They are found on hundreds of volcanic islands that have never been connected to any landmass. Several examples of highly vagile species can be found, the most notable being the Monarch (*Danaus plexippus*) which regularly crosses the Atlantic from North America into Europe. *Vanessa cardui* is a strong flier and has an almost cosmopolitan distribution with the exception of South America (Larsen 2005). There are examples of long-distance colonization, including between India and Madagascar (Zakharov et al. 2004; Kodandaramaiah and Wahlberg 2007). It is beyond doubt that Madagascar and Australia-New Guinea have been colonized multiple times from Africa and the Oriental region respectively. On the contrary, vicariance at the continental level has received very little evidence in published studies. It is thus safe to assume that butterflies have a much higher probability of transoceanic dispersals than amphibians. Hence, if divergence times were much earlier than the timing of Gondwanan events, a Gondwanan origin for a group of butterflies with the same distributions as the frogs in the previous example would be much less justified. A scenario of transoceanic dispersals is as probable, if not more. DIVA would completely ignore the difference in vagility between the two groups. Indeed, Von Bocxlaer et al. (2006) found that DIVA inferred three improbable dispersals from Madagascar to Eurasia. The analytical method treated their taxon as it would any other highly vagile group. The rigor of their biogeographic hypothesis hinges very little on the analytical method used, but largely on the knowledge of the ecology and life-history of their taxon. Why should such information not be included in the analysis itself before hand?

Figure 1 depicts a simplified Taxon-Area-Cladogram (TAC; where taxa are replaced by their distributions) for Natatanura. I reanalyze this TAC using a modified version
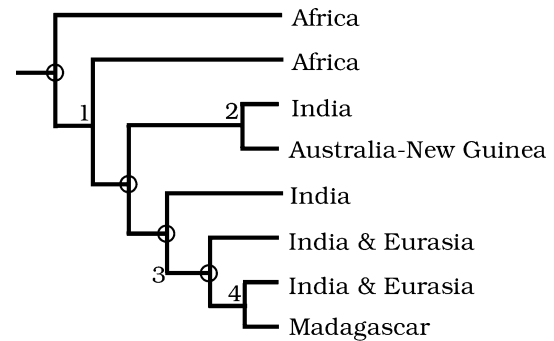


**Fig. 1** Simplified Taxon-area-cladogram (TAC) of Natatanura from Van Von Bocxlaer et al. (2006). Numbers 1, 2 and 4 indicate inferred vicariance or dispersal events, depending on the whether the scenario is Gondwanan origin or Out-of-Africa origin. 1: between Africa and India. 2: between India and Australia-New Guinea. 3: between India and Madagascar. 4: dispersal along the branch between India and Eurasia following the collision of the Indian plate with Eurasia. Circles indicate within-area speciation events

of Dispersal-Vicariance optimization for both amphibians and a hypothetical butterfly group. Transoceanic dispersals are assigned a cost of ten for amphibians and four for butterflies. Because all divergence time estimates are younger than well-accepted timing estimates for Gondwanan rifting events, vicariance is assigned a general cost of five for both groups. Overland dispersal from India to Eurasia are presumed to have a higher probability than oceanic dispersal, hence the former receive a cost of two. No cost is assigned to within-area speciation events.

Two hypotheses—Gondwanan origin and Out-of-Africa origin—are compared for the two groups (Table 1). A scenario of Gondwanan origin similar to that reported by Von Bocxlaer et al. (2006) receives lesser total cost for amphibians. For butterflies, an origin in Africa is a better scenario. In this scenario, they dispersed into India, followed by subsequent dispersal into Australia-New Guinea. There was a dispersal into Eurasia when India collided against it. There was another transoceanic dispersal to Madagascar. Hence, with more realistic costs, an out-of-Africa origin followed by global dispersals is a more likely explanation for butterflies. Although not exactly the same, the distributions of this hypothetical group of butterflies is similar to some real groups of butterflies, for e.g., the genus *Junonia, the Papilio demoleus* species group and the sub-tribe Mycalesina.

This example illustrates that changing the costs in Dispersal-Vicariance optimization to reflect differences in vagility can drastically affect inferences of vicariance and dispersal. It also illustrates the point that completely congruent area cladograms do not always translate to evidence for speciation driven solely by vicariance if the taxa in question have different vagility potential.

**Table 1** Costs for two hypotheses of origin for the TAC depicted in Fig. 1

|  | Amphibians Gondwanan vicariance | Out-of-Africa dispersal | Butterflies Gondwanan vicariance | Out-of-Africa dispersal |
|---|---|---|---|---|
| 1 | 5 | 10 | 5 | 4 |
| 2 | 5 | 10 | 5 | 4 |
| 3 | 2 | 2 | 2 | 2 |
| 4 | 5 | 10 | 5 | 4 |
| Total | 17 | 32 | 17 | 14 |

Assumptions: Vicariance costs 5; overland dispersal costs 2; within-area speciation costs 0; transoceanic dispersal costs 10 for amphibians and 4 for butterflies. Numbers indicate nodes or branches involved in the event (see Fig. 1)

## Example 2

Braby et al. (2005) inferred the phylogeny of a group of swallowtail butterflies (Papilionidae: Troidini) using molecular markers and attempted to reconstruct the history of the group using Dispersal-Vicariance optimization. These butterflies are distributed in the Oriental, Neotropical and Australasian regions in addition to a monotypic genus in Madagascar. They ignored previous age estimates (de Jong 2003) that suggested the group was too young to be Gondwanan in origin. Instead they conclude that the subtribe Troidina had its origin in Gondwana and diverged vicariantly from a single widespread ancestor. This hypothesis rests solely on the fact it involves the least number of dispersal events. They go on to use the timing of the split between India and Madagascar to calibrate their estimates of lineage divergence times. A more recent molecular study (Nazari et al. 2007) that used both geological and fossil calibration points indicated a much earlier age for the first split within Troidina (<60 mya), corroborating previous estimates.

Their conclusion of an origin in Gondwana has several problems. First and foremost, they implicitly assume that dispersal is much less likely than vicariance for butterflies, thereby implying that butterflies have poor vagility. Birdwing butterflies, which possess the largest wingspan among all butterflies (Parsons 1998) are part of Troidina. All genera in Troidina apart from *Pharmacophagus* (which is restricted to Madagascar) are distributed over several regions separated by oceanic barriers. As an example, *Pachliopta* ranges from Southern India through Indo-China and islands in South East Asia to New Guinea, Australia and islands of the Solomon Archipelago. Without doubt, these species, like most other butterflies, have few problems dispersing across oceanic and land barriers given millions of years. Hitherto well accepted hypotheses of Gondwanan vicariance have been time and again rejected in favour of dispersal by robust age estimates (e.g., McDowall 2002; Raxworthy et al. 2002; Renner 2004; Richardson et al. 2004; Cook and Crisp 2005b; Knapp et al.

2005; Yoder and Nowak 2006; Trénel et al. 2007; Grandcolas et al. 2008). Yet, vicariance events have been invoked in this highly vagile group and even used to calibrate age estimates. Furthermore, the order of break-up of Gondwanan fragments does not fit with the relative ages of splits between lineages. Their reconstruction indicates that four species in India (ancestor of *Atrophaneura + Pachliopta*), Australasia (two ancestors, of *Cressida* and *Ornithoptera + Troides*) and South America (ancestor of *Euryades + Parides*) started diverging almost simultaneously from a single widespread species a few million years after *Pharmacophagus* diverged in Madagascar (Fig. 21 in Braby et al. 2005). How did the ancestor of Troidina come to be distributed over India, Australia and South America, landmasses that began rifting >120 mya, ca. 35 mya and 30 mya, respectively (McLoughlin 2001)? This is a clear example of a vicariance-centric assumption that ancestors were extremely widespread but the descendants are not (Bremer 1992; Ronquist 1997).

I reanalyze their dataset using a protocol similar to that used in the first example. Taking into account age estimates in Nazari et al. (2007) and de Jong (2003), oceanic dispersals are more likely than ancient vicariance events. Extinctions are assigned a cost of five. Figure 2 depicts the TAC for Troidina, derived from Figs 21 and 22 in Braby et al. (2005). I compare the hypothesis presented by Braby and colleagues to the hypothesis that Troidina started diverging in the Oriental region and diversified through dispersal (Zeuner 1943; Holloway and Jardine 1968). Here, the origin of the *Euryades-Parides* clade in South America is explained by a dispersal from Australia across Antarctica before the latter became glaciated (which began ca. 30 mya; McLoughlin 2001). Costs of events for both hypotheses are tabulated in Table 2. The Gondwanan hypothesis in Braby et al. (2005) receives a total cost of 35 whereas the Oriental hypothesis receives 24. The latter better explains how lineages in India, Australia and South America started diverging almost simultaneously. A single vagile ancestor managed to disperse from the Oriental region to Australia and South America over the timespan of
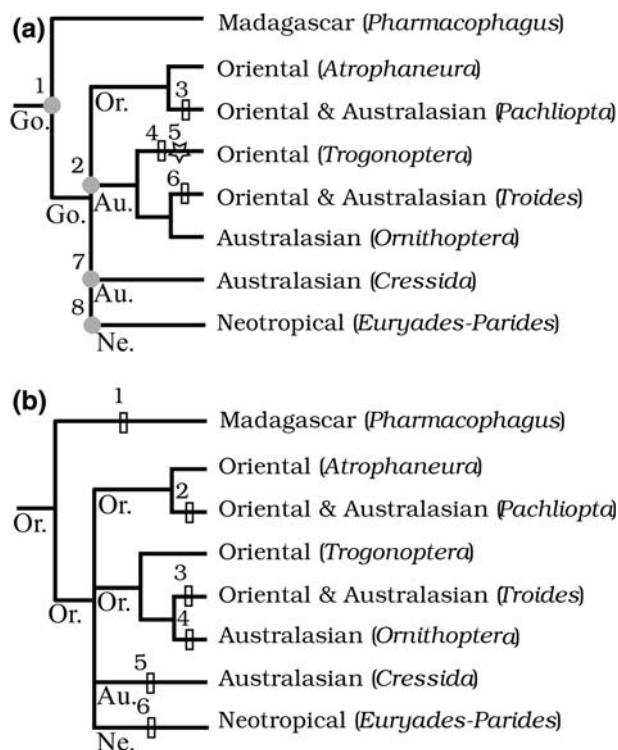
**Fig. 2** Taxon-area-cladogram of Troidina derived from Figs. 21 and 22 in Braby et al. (2005) with biogeographic events indicated according to two hypotheses, Gondwanan origin and Oriental origin. *Circles*, *rectangles* and *stars* indicate vicariance, dispersal and extinction respectively. Numbers above the events are those used in the description of the event in Table 2a. **a** Inference based on the assumption that the ancestor was widespread over Gondwana. **b** Inference based on the assumption that the clade started diverging in the Oriental region following the break-up of Gondwana

**Table 2** Costs for two hypotheses of origin for the TAC depicted in Fig. 2, where vicariance receives a cost of 5 and dispersal 4

| | Event | Cost |
|---|---|---|
| (a) Gondwanan origin | | |
| 1 | Vicariance: Madagascar | 5 |
| 2 and 7 | Vicariance: Australia | 5 |
| 3 | Within-genus dispersal: Oriental to Australasia | 5 |
| 4 | Within-genus dispersal: Australasia to Oriental | 5 |
| 5 | Extinction: Australasia | 5 |
| 6 | Dispersal: Australasia to Oriental | 5 |
| 8 | Vicariance: Neotropical | 5 |
| Total cost | | 35 |
| (b) Oriental origin | | |
| 1 | Dispersal: Oriental to Madagascar | 4 |
| 2 | Within-genus dispersal: Oriental to Australasia | 4 |
| 3 | Within-genus dispersal: Oriental to Australasia | 4 |
| 4 | Dispersal: Oriental to Australasia | 4 |
| 5 | Dispersal: Oriental to Australasia | 4 |
| 6 | Dispersal: Australasia to Neotropical | 4 |
| Total cost | | 24 |

a million years or so, and diverged allopatrically. This is quite plausible, and supported by numerous examples from butterfly genera with endemic species in more than three continents (e.g., *Junonia, Hypolimnas, Vanessa, Euploea, Papilio, Colias,* etc.). The Oriental hypothesis is also consistent with the observation that *Troides* has its highest diversity in the Oriental region, with a single species in Australasia that does not extend into the Australian mainland (Parsons 1998; Braby et al. 2005). According to the scenario in Braby et al. (2005), *Troides* was a Gondwanan relict that later dispersed into South East Asia.

How true the scenario described here is depends strongly on the realism of the weighting scheme implemented in the analysis. The software DIVA uses costs that are heavily prejudiced against dispersal scenarios irrespective of how vagile the taxon of interest is. On the other side of the coin, assigning unrealistically low costs to dispersal can result in *ad hoc* hypotheses of dispersal where vicariance would be a more rational explanation. In the troidine example, equal costs for vicariance and dispersal,

i.e., 5 v/s 5, leads to a total cost of 30 for the Oriental hypothesis and 35 for the Gondwanan hypothesis. Costs of 4 v/s 5 (vicariance v/s dispersal) result in total costs of 30 v/s 32 (Oriental v/s Gondwana). Generally, costs in the ratio of 4:5 (vicariance:dispersal) or greater favour the Oriental hypothesis and in the ratio of 3:5 or lesser favour a Gondwanan vicariance scenario.

The critical issue is what weighting scheme should be assumed during an analysis. Where available, information from metapopulation, population genetic or phylogeographic studies could be harnessed to obtain an idea of dispersal rates between specific areas. Assuming that genera are monophyletic, the geographic spread of genera themselves can provide an idea about the dispersive powers of species in the group. If a group has a number of genera with species in several zoogeographic regions, this is indicative of good vagility of the group. However, genera are inconsistent taxonomic groupings; thus groups with restricted genera are not necessarily poor dispersers but might simply contain fewer species. Species distributional ranges themselves can offer insights into the kinds of barriers that are easy to colonize across and those that are insurmountable. Unless there is strong *a priori* reason to believe that the taxon of interest cannot cross a barrier, it is perhaps best to begin with equal costs for dispersal and vicariance and try out a range of weighting schemes. However, vicariance can be assigned a cost of zero where ages of divergences concur with geological events that can cause vicariance. It is also worthwhile to compare results with Dispersal-Vicariance analyses on other taxa present in

the area. Vicariance inferences are greatly fortified if they are also found independently in other taxa.

One might argue that implementing a weighting scheme in Dispersal-Vicariance optimization based on the presumed vagility can easily lead to unreal, *ad hoc* hypotheses of dispersal. However, current costs implemented in DIVA are themselves arbitrary and lack justification for groups with good dispersive power. In light of this, why should we not *attempt* to make them more realistic? Another philosophical problem of assuming differential vagility potential *a priori* is the risk of losing the power to test how vagility affects modes of evolution using historical biogeographic analyses. For instance, we cannot invoke vagility as an explanation for discordant patterns between taxa if we have already assumed that they have different vagility. I believe this is a small cost compared to the prospect of inferring a spurious biogeographic history.

## Conclusion

Donoghue and Moore (2003) suggest that analytical methods in historical biogeography have given us few genuinely new insights. In contrast, Crisci (2001), in his review of methods in historical biogeography, opines 'We have made enormous strides in the past few years; in other words, we have started to babble in the language with which the traces of the past are telling us the history of life on earth….'. Although many conceptual and methodological advances have been made, I believe we are still not in a position talk with confidence. I argue that vagility should be explicitly taken into account in all historical biogeographic analyses in order to improve the realism of reconstructions. When using methods that seek shared patterns among several co-occuring taxa, it is imperative that taxa with similar ecological traits are analyzed together. In event-based analyses of individual taxa, the effect of vagility on the relative probabilities of different speciation modes should be taken into account rather than assuming a single set of costs for all taxa and all geological scenarios. Furthermore, I believe hypotheses of vicariance from such individual analyses become more robust when they are corroborated by other taxa in the area with similar ecological attributes.

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