



# Phylogenetic comparative methods and the geography of speciation

Jonathan B. Losos and Richard E. Glor

Department of Biology, Campus Box 1137, Washington University, St Louis, MO 63130-4899, USA

**The geography of speciation has long been contentious. In recent years, phylogenetic approaches have been proposed to determine the geographical mode of speciation. If reliable, these methods not only provide a means of settling the debate about the geography of speciation, but also indicate that sympatric speciation is surprisingly common and that peripatric speciation is relatively rare. Similar to any phylogenetic inference, reconstructions of speciation mode are only useful if the underlying assumptions of the method are met. In this case, the key assumption is that the geographical range of both extant and ancestral species at the time of speciation can be inferred from present-day distributions. We discuss whether, and under what circumstances, such assumptions could be met. We conclude that interspecific phylogenies are unable to test alternative hypotheses concerning the geography of speciation rigorously because of the lability of geographical ranges and the lack of correlation between the role of adaptive processes and geographical mode of speciation.**

In spite of half a century of research, resolution of the controversies concerning the manner in which SPECIATION (see Glossary) occurs does not appear to be imminent [1]. Given the great success of phylogenetic approaches over the past 15 years in addressing a wide variety of evolutionary questions (e.g. [2–6]), attempts to apply these methods to the study of speciation are not surprising (reviewed in [7]).

Spurred by Lynch's influential paper [8], recent studies have attempted to use interspecific phylogenetic comparative methods to address one of the most contentious issues in speciation: the geographical mode of speciation [2,9–24]. The results of such studies have attracted considerable attention, both for their promise of resolving long-standing questions and for their unexpected findings, such as the suggestions that PERIPATRIC SPECIATION is relatively rare and that SYMPATRIC SPECIATION is surprisingly common [2,8,11,14,19]. If reliable, these methods at last provide an effective approach toward settling disputes about the frequencies of different geographical modes of speciation. However, if the assumptions of these methods are not met, the resulting conclusions might not be reliable. Here, we assess the extent to which these assumptions are realistic and evaluate the contribution

that such phylogenetic approaches can make to the study of the geography of speciation.

## Phylogenetic approaches and the geography of speciation

### *Methods and assumptions*

Most interspecific phylogenetic approaches to the geography of speciation work by examining the distribution of sister taxa: for example, if they are sympatric, then speciation is inferred to have been sympatric and if they are allopatric, speciation is inferred to have been allopatric (Fig. 1). For extant taxa, this approach leads to the comparison of sister species; for deeper nodes in a phylogeny, the procedure becomes more complicated because the geographical distribution of ancestral taxa must first be inferred (Box 1).

The Achilles heel of this approach is that it requires the reconstruction of the geographical distribution of species at the time of speciation. The obvious problem with this approach is that the current distribution of a species is not necessarily a reliable indicator of the historical geographical range of the same species (K.A. Crandall, PhD thesis, Washington University, 1993, [8,9,14,24,25]). One need only consider the alteration of the ranges of species that occurred during and after the Quaternary 'Ice Ages' to recognize how radically ranges have shifted in recent evolutionary history, not only in glaciated areas [26–28], but also in tropical forests and oceans [29–31].

Three lines of evidence indicate that the geographical range of species can, and often does, change substantially over short periods of time because of climate change, colonization of new areas, extinction of competitors, and a host of other reasons. First, the fossil record documents the

## Glossary

**Allopatric speciation:** speciation resulting from divergent evolution of populations that are geographically isolated from each other.

**Parapatric speciation:** speciation resulting from divergent evolution of populations that are geographically adjacent to each other.

**Peripatric speciation:** a subset of allopatric speciation in which a peripherally isolated population diverges to become a new species.

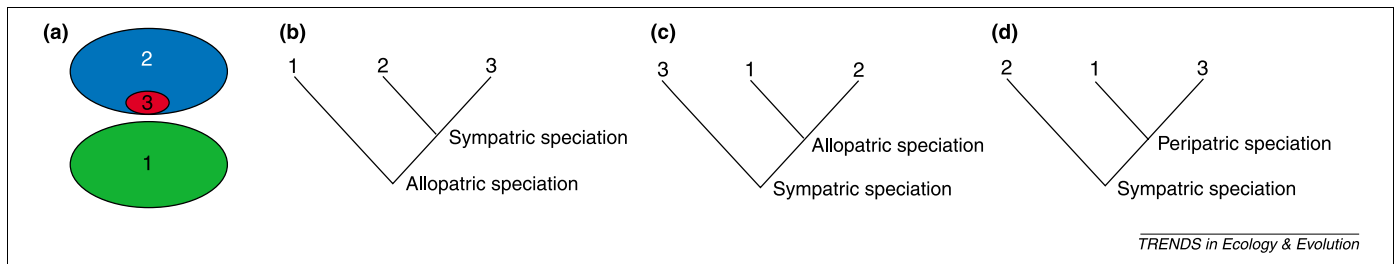
**Peripheral isolates:** a geographically isolated population on the periphery of a species' range.

**Speciation:** divergent evolution resulting in two species from an initial ancestral species.

**Sympatric speciation:** speciation occurring within a single geographical area.

**Vicariant speciation:** a subset of allopatric speciation in which two populations become isolated by the fragmentation of an initially continuous range into two or more allopatric populations, each of which is substantial in size (i.e. neither is a peripheral isolate).

Corresponding author: Jonathan B. Losos (losos@biology.wustl.edu).



**Fig. 1.** Testing hypotheses with interspecific phylogenies. Current geographical distributions of three species (a) are used to infer geographical modes of speciation. When species that overlap geographically are sister taxa (b), sympatric speciation is inferred. When sister species do not overlap geographically (c), sympatric speciation is rejected and allopatric speciation is inferred. When sister species do not overlap and the range of one is smaller than the range of the other (d), peripatric speciation is inferred.

occurrence of range shifts through time: some extant species are now found in localities in which they did not occur prehistorically, and vice versa [32–40]. Second, observational studies in historical time have directly documented countless changes in geographical distributions [26,41–46]. Third, population genetic analyses routinely uncover evidence for geographical range expansions (e.g. [47,48]). As a result, the present-day range of a species will often differ greatly from the range of that species when it first arose; for this reason, several authors have concluded that evolutionary inferences concerning the geography of species in the past will often not be reliable [14,41,49–51].

These concerns are magnified further when attempts are made to reconstruct the geographical speciation mode of ancestral taxa (e.g. [8,9,19,21,22]). Recent studies have revealed that, under many circumstances, phylogenetic comparative methods are unable to reconstruct ancestral traits accurately; this is particularly true when the trait is evolutionarily labile, such that the rate of trait evolution is high relative to the rate of speciation [52–54], as might be the case for geographical range. Moreover, inferences about the geographical distributions of ancestral taxa deduced from the ranges of their descendants are based on a method that does not seem very robust (K.A. Crandall, PhD thesis, Washington University, 1993, [25]): this method reconstructs the geographical range of an ancestral species as the sum of the ranges of its descendants (Fig. 2, Box 2). These reconstructions thus not only assume that geographical ranges of species remain constant after

speciation, but also that entire clades do not experience range contraction or expansion and that extinction does not occur [2,15,55,56].

#### *Allopatric versus sympatric speciation*

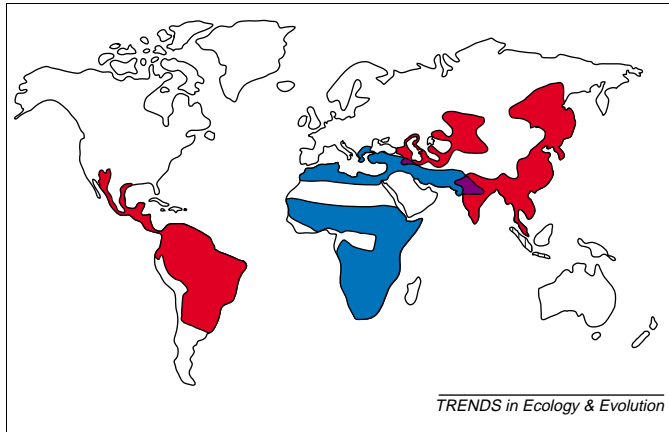
Because of the unreliability of inferences of geographical ranges in the past, interspecific phylogenetic approaches are unlikely to add much to the debate over sympatric versus ALLOPATRIC SPECIATION. Consider first sympatric speciation. Can a null hypothesis that speciation was not sympatric be rejected if sympatric species are found to be sister taxa? Given the potential for the evolutionary lability of geographical range, the finding that sympatric species are sister taxa does not strongly refute the alternative possibility that the species speciated in allopatry or parapatry and subsequently expanded their ranges to come into sympatry. Indeed, this is the heart of the classic debate about sympatric speciation: proponents note that sympatric species are closely related and infer that sympatric speciation has occurred; detractors consider sympatric speciation to be unlikely on theoretical grounds and consider allopatric speciation followed by range expansion to be a more probable explanation [56,57]. Thus, phylogenetic approaches to the study of putative cases of sympatric speciation really do no more than test the usually implicit assumption that the sympatric species truly are sister taxa. Finding that the two species are not sister taxa would, of course, undermine support for a sympatric speciation scenario (e.g. [24,58,59]), but finding that they are sister taxa would not address the primary

#### **Box 1. Phylogenetic reconstruction of the geographical mode of speciation**

Phylogenetic approaches to the geography of speciation (e.g. [2,8,56,78]) use present-day geographical distributions and phylogenetic relationships to infer the geographical context of speciation. In this approach, the current distribution of an extant taxon is used as a character state and comparison of the range of sister taxa enables a decision to be made about which mode of speciation was involved. For extant sister species, present-day distributions are compared and their size and extent of the overlap of the ranges is used to infer geographical mode of speciation. For example, sister species with broadly overlapping ranges would be inferred to have originated by sympatric speciation, whereas sister species in which the ranges were nonoverlapping and in which the range of one taxon was relatively small (<5%) compared with the range of the other species would be considered as evidence of peripatric speciation. Precise criteria for distinguishing geographical modes differ among authors. For example, Mattern and McLennan [19] consider any overlap among the ranges of sister taxa to be indicative of sympatric speciation, whereas Lynch [8] considers <20% overlap to be trivial.

When one or both of the sister taxa are ancestral nodes in a phylogeny, the geographical range of these ancestral taxa must be inferred before sister-taxon comparisons can be made. In this case, the ancestral taxon is assigned a geographical distribution that encompasses the distribution of all of its descendants [8,12,56,78]. Then, the ranges of sister taxa are compared in the same manner as are those ranges of extant sister species.

For the phylogenetic method to provide accurate inferences about speciation, two related assumptions must be met. First, when comparing sister species, one must assume that the current geographical distribution correlates strongly with the geographical distribution at the time of speciation. Second, to infer the geographical distributions of ancestral taxa, one must assume that distributions are so static that ancestral geographical ranges can be inferred from the ranges of their descendants [2,8,15,56,71]. Because of the restrictive nature of this latter assumption, even some proponents of these methods recommend focusing on more recent divergence events (e.g. [8]).



**Fig. 2.** Geographical ranges of lions (*Panthera leo*), tigers (*P. tigris*) and jaguars (*P. onca*). Mattern and McLennan [19] reconstructed speciation modes in a study of feline evolutionary diversification and concluded that sympatric speciation was the most common mode of speciation in cats. For example, they concluded that the lion is the sister taxon to a clade comprising the tiger and the jaguar. The ranges of the lion (blue) and tiger–jaguar (red) clades overlap in western Asia (purple) and the species differ ecologically, leading to the conclusion that the split between these two lineages occurred through sympatric speciation (historical range of lion and tiger are based on maps from [77]). Through this sort of reasoning, the authors conclude that sympatric speciation accounted for 51.8% of felid speciation events, even though they acknowledge that felines are ‘large, highly mobile creatures’ and that the assumption that ‘postspeiation dispersal does not overwhelm speciations patterns’ might have ‘been violated to some extent’. Note that this is an extreme version of the phylogenetic method. Other proponents of this method (e.g. [8]) might not consider the range overlap substantial enough for a claim of sympatric speciation.

concerns of critics, which do not hinge on the evolutionary relationships of the taxa.

For these reasons, interspecific phylogenetic studies by themselves add little support to claims of sympatric speciation (or for claims of PARAPATRIC SPECIATION, to which the same criticisms apply). For example, vertebrates, particularly species that tend to be highly mobile, have always been considered to be unlikely candidates for sympatric speciation. Hence, phylogenetically based studies that concluded that 52% of speciation events in felids [19] (Fig. 2) and > 20% of speciation events in birds [8,14,16] were the result of sympatric speciation were quite surprising. In light of the potential lability of geographical range discussed above, we suspect that we are not alone in finding these results unconvincing (see [14] for similar conclusions from a detailed analysis of 13 avian clades).

This is not to say, however, that phylogenetic studies can never be used to make a case for sympatric speciation; combined with additional evidence that argues against a scenario of nonsympatric speciation followed by range expansion, phylogenetic studies can make the case for sympatric speciation more compelling [10]. The best documented such case involves two crater lakes in Cameroon, each of which is occupied by its own clade of cichlid fish [60] (Fig. 3). The most parsimonious conclusion is that, in each crater, a single ancestral species colonized the crater and subsequently speciated repeatedly. The topographical and ecological homogeneity of these small (< 5 km<sup>2</sup>) craters suggests few opportunities for allopatric speciation; indeed, it is situations such as this, in which an allopatric phase of differentiation seems inconceivable, that have prompted many claims of sympatric speciation in the literature. The most plausible allopatric scenarios would require either that ancestral populations became geographically isolated in these tiny and apparently homogeneous lakes (cf. [61,62]) or that each of the 20 species in the two lakes was the result of dispersal by related species that lived outside of the lake and that subsequently went extinct, thus rendering the lake species monophyletic relative to other extant species. Such scenarios are plausible, although less parsimonious than a straightforward hypothesis of sympatric speciation.

Although phylogenetic studies have suggested surprisingly high rates of sympatric speciation, allopatric speciation is still usually identified as the predominant mode in such studies [8,9,14,63]. This result is not surprising because the taxa in most phylogenetic studies apparently were chosen, not because they had been suggested as potential cases of nonallopatric speciation, but rather because data about geographical ranges and phylogenetic relationships were available for those taxa. If allopatric speciation is the predominant mode of speciation in most types of animal, as most workers believe, and if study taxa are chosen randomly with respect to likelihood of speciating in a particular manner, then one would expect to find a predominance of cases of allopatric speciation.

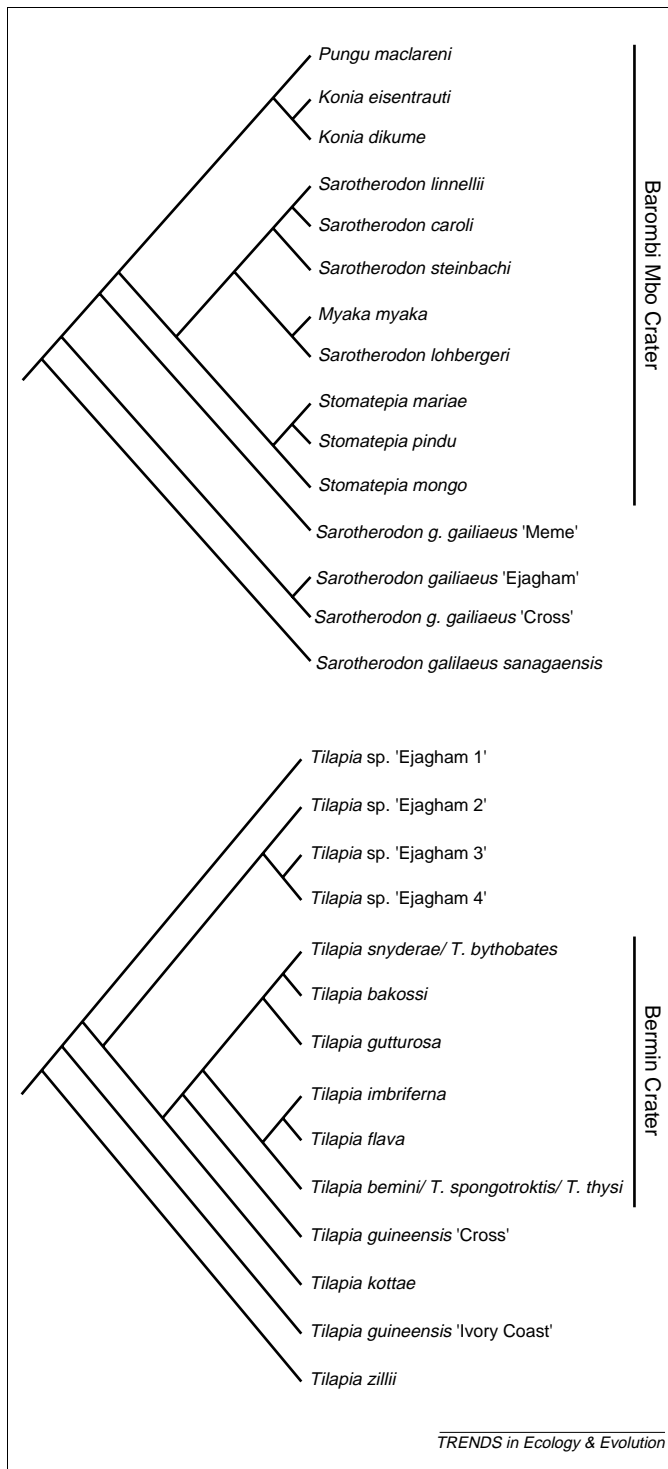
However, for the same reasons discussed with regard to sympatric speciation, finding that sister taxa are allopatric is not definitive support for allopatric speciation; sympatric speciation followed by range shifts leading to allopatry

### Box 2. The relationship between geographical modes of speciation and adaptive evolution

As a corollary to phylogenetic approaches to the geography of speciation, several workers [12,13,16] have suggested that not only the geographical mode of speciation, but also the underlying process driving speciation, can be determined from examination of phylogeny. In particular, they argue that some modes of speciation, such as peripatric speciation, involve adaptive evolution, whereas other modes, such as vicariant speciation, do not. However, this assumption is unwarranted – no relationship necessarily exists between the geographical mode of speciation and underlying evolutionary process [79].

Although parapatric and sympatric speciation almost certainly involve adaptive processes, vicariant speciation and peripatric speciation have no necessary relationship with adaptive versus nonadaptive evolutionary processes. For example, field and laboratory studies

indicate that allopatric populations are more likely to speciate when selection causes their adaptive divergence [80–83]. Consequently, evidence favoring the vicariant mode of geographical speciation does not constitute evidence that adaptation was not involved in the speciation process; quite the contrary, these studies indicate that vicariant speciation is more likely when adaptation is involved. Furthermore, founder-induced or peripatric speciation does not require that the daughter species undergo adaptive divergence [84]. For example, Powell [85] used experimental studies to argue that founder effects might lead to pre-mating isolation among populations of *Drosophila pseudoobscura* without accompanying adaptive divergence. Hence, at least in allopatric speciation, no relationship exists between the mode of speciation and the extent of adaptive divergence during the speciation process.



**Fig. 3.** Phylogenies of cichlid species from two small African crater lakes. The monophyly of species in each crater and the lack of obvious barriers to gene flow within them makes sympatric speciation the most plausible interpretation. Reproduced, with permission, from [60].

could produce the same present-day pattern. Indeed, fossil data reveal cases in which currently allopatric species were sympatric in the late Pleistocene [37]; moreover, some species of plants that are likely to have arisen sympatrically by allopolyploidy now have allopatric distributions separated by hundreds of kilometers [10]. As for sympatric speciation, the inclusion of additional data can make a case for allopatric speciation compelling.

<http://tree.trends.com>

For example, when sister taxa occur on different islands [64,65], are separated by physical barriers (e.g. [66]), or share a common pattern of geographical distribution with other sets of sister taxa [23], then allopatric speciation would seem to be the most probable interpretation.

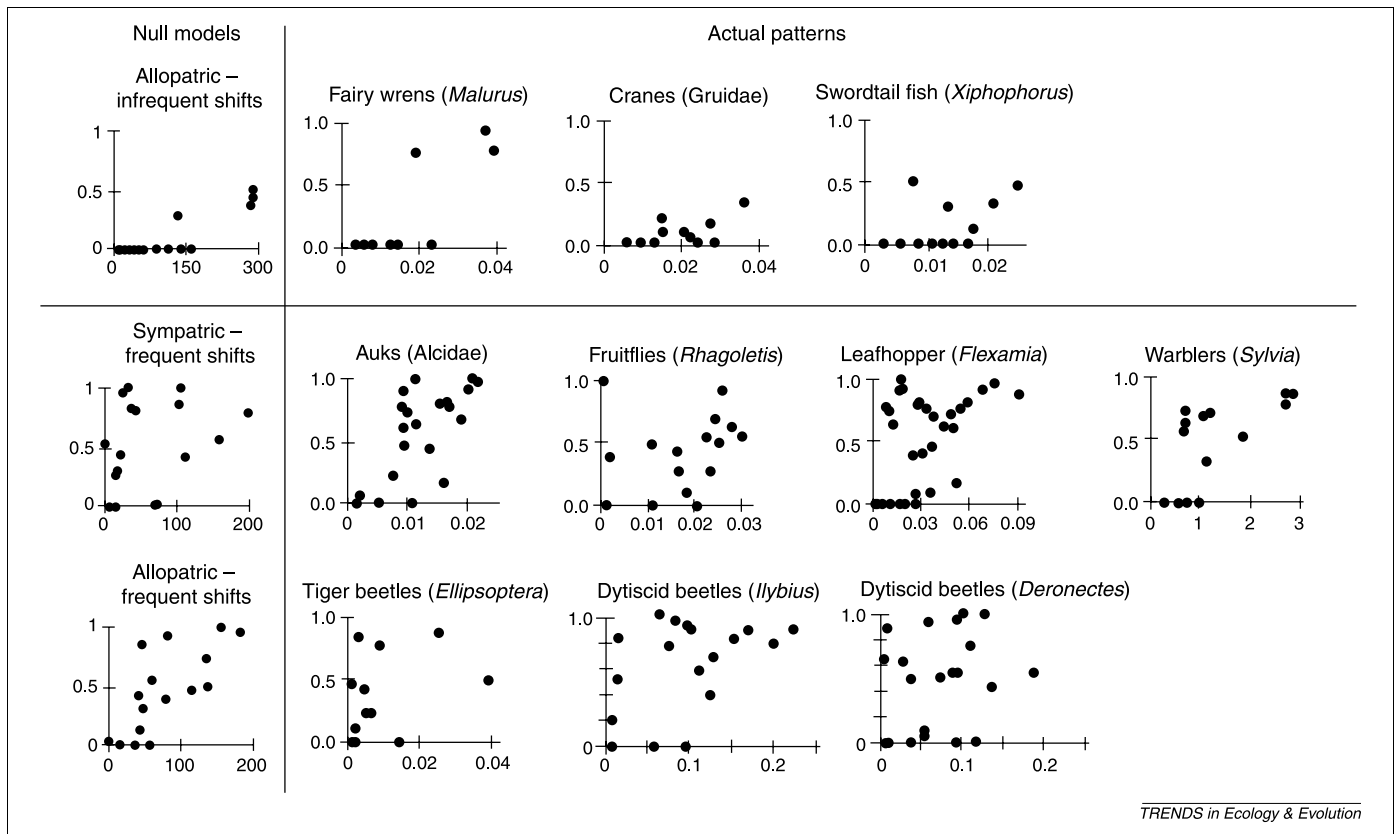
#### *Vicariant versus peripatric speciation*

Several studies have extended the approach outlined above to distinguish between different types of allopatric speciation (e.g. [8,9,16]). In this case, it is the relative size of the ranges of species at the time of speciation that distinguishes between peripatric (or PERIPHERAL ISOLATES) and VICARIANT SPECIATION; similarly sized ranges indicate vicariant speciation, whereas asymmetric range sizes indicate peripatric speciation (Fig. 1). For the same reasons as discussed above, however, inferences about ancestral geographical range size are unlikely to be accurate in many circumstances, and hence phylogenetic comparative methods might provide little insight [14]. Moreover, if Chesser and Zink [14] are correct that only those peripatrically derived species that rapidly expand in range size are likely to survive, then this method will not only be inaccurate, but also biased against detecting peripatric speciation.

Another approach for distinguishing peripatric from vicariant speciation was proposed recently by Chan and Moore [13], who suggested that measures of tree balance could be used to distinguish between the two. In a nutshell, Chan and Moore [13] argue that vicariant speciation will produce more balanced tree topologies than will peripatric speciation because, in peripatric speciation, the processes leading to speciation occur solely in the peripheral population. Consequently, one daughter species (the peripheral populations) must complete the speciation process before being able to speciate again, whereas the other (the main population) can speciate again immediately; thus, the latter clade will tend to accumulate more speciation events, leading to an unbalanced phylogenetic topology. By contrast, in vicariant speciation, the speciation process will affect both populations equally, and thus no consistent difference should exist in the time at which either is able to speciate again; as a result, more symmetrical phylogenetic topologies would be expected. However, this method assumes allopatric speciation from the outset and cannot distinguish between allopatric, parapatric and sympatric speciation; similar to vicariant speciation, parapatric and sympatric speciation should also produce balanced tree topologies because these speciation processes should affect both daughter species in the same way. Moreover, many other explanations, such as the evolution of characters that promote speciation, have been put forward to explain tree imbalance [67–70]; thus, the existence of imbalance, even in clades in which allopatric speciation seems to have occurred, would not necessarily be indicative of peripatric speciation.

#### *Patterns of character evolution*

Patterns of character evolution have also been suggested as a line of evidence that can support geographical interpretations (e.g. [15,16,71]), but such approaches are fraught with assumptions and are unlikely to be generally



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**Fig. 4.** Plots of geographical range overlap through time. In three out of ten actual phylogenies [fairy wrens (*Malurus*), cranes (Gruidae) and swordtail fish (*Xiphophorus*)], most comparisons among recently divergent taxa are allopatric [as indicated by the percent range overlap (x-axis) versus evolutionary age (y-axis)], a signature of allopatric speciation with infrequent range shifts (although the swordtail fish do not show the predicted steady increase in overlap with age). However, the remaining seven groups closely resemble the results of null models that assume frequent range shifts, conditions under which allopatric and sympatric null models are indistinguishable. The inability to distinguish the observed patterns from those produced by the null models suggests that inferences concerning the geographical mode of speciation cannot be made reliably. Reproduced, with permission, from [9,21].

applicable. For example, Friesen and Anderson [16] suggest that vicariant speciation can be ruled out for taxa that exhibit relatively high rates of character change because such high rates are the signature of adaptive differentiation, which is supposed to not be involved in vicariant speciation. However, other processes can produce high rates of character change and adaptive differentiation might play an important role in vicariant speciation (Box 2). We suspect that no general relationship exists between patterns of character evolution and the geographical mode of speciation.

### Shifts in range overlap through time

Several studies have used phylogenies to test geographical modes of speciation by examining changes in geographical range size and overlap of sister taxa through time [8–10,21,24] (Fig. 4). If, for example, allopatric speciation is predominant, then recently diverged sister taxa will tend to be geographically nonoverlapping, and the degree of overlap is likely to increase between deeper phylogenetic clades as a result of geographical range shifts. Conversely, if sympatric speciation is the norm, then recent sister taxa will be entirely overlapping, but sister clades deeper in the tree will be more likely to have shifted their ranges and thus overlap less. Similar reasoning is used to distinguish peripatric from vicariant speciation. This test is a significant advance over previous methods because it does not require the reconstruction of

ancestral geographical ranges. However, it is based on the assumption that, because geographical ranges shift over time, the geographical signal of speciation decays with age such that the deeper one looks in a phylogeny, the less sister taxa will exhibit a geographical pattern that conforms to the geographical mode of speciation they experienced.

Barraclough and Vogler [9] conducted an important test of this approach by using simulations to assess what patterns would be expected for a phylogeny given different modes of speciation and different rates of geographical range change. These models suggest that, when a particular mode of speciation predominates in a particular group and ranges shift stochastically following speciation, modes of speciation can be inferred by plotting range overlap versus evolutionary age (Fig. 4). However, these null models also indicate that, when rates of geographical range change are high, it will be impossible to distinguish among different geographical modes of speciation because range shifts will obscure the geographical pattern of speciation for even the most recent events (Fig. 4).

In an examination of actual phylogenies, Barraclough and Vogler [9] found that, although many sister species are allopatric and range overlap increases with age in some groups, suggesting allopatric speciation, this correlation is always weak and confidence limits around the y-intercept, which represents geographical overlap at time of speciation, are often very large. Unfortunately, in most groups,

the correlation between evolutionary age and geographical overlap is indistinguishable from simulations that incorporate high rates of geographical range change, regardless of whether the geographical mode of speciation in the simulations is allopatric or sympatric [9,21] (Fig. 4). In other words, the pattern frequently observed in real phylogenies cannot be used to make inferences about the geographical mode of speciation. Given that the true rate of change in geographical range will usually be unknown and, in many cases, might be large, drawing firm conclusions from these studies will be difficult. The one exception is groups in which almost all sister taxa are allopatric and in which only sister taxa deep in the tree exhibit geographical overlap [24] (Fig. 4). In such cases, a conclusion that allopatric speciation has occurred is reasonable, although it seems unlikely that, even in the absence of these methods, anyone would have considered such geographical patterns to be the result of any other mode of speciation.

In summary, Barraclough and Vogler find that, under the conditions of their null model, allopatric speciation and sympatric speciation can be distinguished by plotting range overlap versus age, but only when range shifts have been relatively infrequent. In practice, few phylogenies present the clear-cut pattern exhibited by the null models, suggesting either that range shifts are too frequent to leave a signature in most groups or that a single mode of speciation rarely dominates in a given group.

### The future of phylogenetics in the study of the geography of speciation

Because speciation occurs at the population/species interface, methods are needed that focus at that level [25,72]. One recent approach has been to use phylogenetic approaches to focus solely on recent divergence events, either between populations within a species or within closely related species (reviewed in [73]). These approaches propose that the phylogenetic structure of genetic variation among populations and very recently diverged species will differ depending on geographical mode of speciation. For example, the finding that a small and geographically isolated population was closely related to a population of a geographically widespread species, rendering that species paraphyletic, might indicate the occurrence of recent peripatric speciation [72]. More work is needed to validate these types of prediction, although the more general concern still remains of whether, even among such closely related taxa, one can assume that post-speciation range shifts have not obscured patterns of speciation.

Other recent approaches have moved even closer toward the population–species interface (Box 3). These historical population genetic methods can estimate several parameters that might be useful in attempts to distinguish among alternative geographical models of speciation, such as historical population size and rates of gene flow, and could also be used to detect the signature of some

#### Box 3. Historical population genetics and the geography of speciation

Coalescent approaches to population genetics have been developed over the past 20 years to examine the historical processes responsible for patterns of genetic variation that exist within and among populations (reviewed in [86]). Some coalescent methods, which have been developed primarily to test demographic, genetic and ecological mechanisms of speciation, might also be useful for testing geographical modes of speciation.

Several methods test the simple null hypothesis of complete isolation of incipient species versus more complex models that involve divergence-with-gene-flow, natural selection, or both [87–90]. Kliman *et al.* [88] applied such an approach to a study of the *Drosophila simulans* complex, finding that a simple isolation model provides a good fit to the divergence between the cosmopolitan *D. simulans* and two island endemic forms, *D. mauritiana* and *D. sechellia*, suggesting the occurrence of allopatric speciation (perhaps not a surprising result given the geographical distribution of these species). By contrast, Machado *et al.* [87] rejected the strict isolation model and found evidence that some gene flow has occurred between *D. persimilis* and *D. pseudoobscura* since these species began diverging, but not recently.

These methods appear to be quite promising for distinguishing among models of isolation, divergence-with-gene-flow, and natural selection when data from multiple independent loci are available. However, this does not necessarily directly translate into distinguishing among alternative geographical modes of speciation (a purpose for which these methods were not originally intended). In the case of *D. persimilis* and *D. pseudoobscura*, support for the divergence-with-gene-flow model might be the result of limited gene flow throughout the speciation process, as might be expected under sympatric or parapatric speciation, or limited gene flow following secondary contact between species whose initial divergence occurred in allopatry. Similarly, selection at some loci, but not others, during species divergence might occur in sympatry or parapatry, or might be the result of secondary contact and reinforcement following speciation in allopatry [89].

In some cases, additional analyses could be used to distinguish

among alternative geographical modes at a finer scale. For example, if the data fit a model of strict isolation, estimation of historical effective population sizes of sister species at the time of speciation might be possible [91]. These estimates could then be used to test the hypothesis of peripatric speciation, which predicts greatly different population sizes in sister species at the time of speciation. Hare *et al.* [92] used this approach to find that historical effective population sizes of two dolphin species with antitropical distributions have been very large throughout their history, which suggests that their divergence did not involve small peripatric populations.

Other methods, such as nested clade analysis [93], directly incorporate haplotype trees with geographical information to test whether phylogeographical associations are due to recurrent gene flow or historical events, such as fragmentation, colonization and range expansion. Such analyses of the dynamical history of the geographical range of a population might sometimes be crucial for discriminating between alternative geographical modes of divergence [93,94]. For example, this method has been used to show that partially overlapping distributions of phylogenetically distinct groups could be due to divergence in allopatry followed by range expansion [93].

Of course, all of the population-level analyses discussed above have assumptions of their own that could limit their ability to answer questions about the geography of speciation [87,92,95]. For example, methods for estimating ancestral effective population sizes assume panmixia in the ancestor and both descendants, an assumption that, when violated, could result in rejection of the isolation model or unrealistic estimates of historical effective population sizes [87,92]. However, historical population genetic approaches will undoubtedly provide fresh new insights into the process of speciation, particularly when coalescent analyses of multiple independent loci are combined with standard phylogenetic or phylogeographical analyses. Advances such as the ongoing application of likelihood and Markov Chain Monte Carlo methods are likely to improve the complexity and utility of these methods even further [87]. Whether these approaches will provide insight into the geography of speciation remains to be seen.

important historical processes, such as population fragmentation and range shifting. These new approaches hold great promise for addressing key questions concerning speciation; whether they can resolve debate about alternative geographical modes of speciation, and avoid the pitfalls described above, remains to be seen.

### Conclusions

The past 15 years have seen a remarkable revolution in comparative biology: phylogenetic historical perspectives have gone from being completely ignored to being ubiquitous. As with many conceptual breakthroughs, however, the pendulum has swung too far the other way and re-examination of the utility of these methods has begun (e.g. [74–76]). Phylogenetic approaches, similar to any other analytical method, have their own particular assumptions. When those assumptions are met, phylogenetic approaches represent powerful approaches for addressing many important questions in evolutionary biology. Conversely, when they are not met, as appears often to be the case here, then interspecific phylogenetic methods generally will not be useful.

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