

# Hypothesis testing in biogeography

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**Often, biogeography is applied only as a narrative addition to phylogenetic studies and lacks scientific rigour. However, if research questions are framed as hypotheses, biogeographical scenarios become testable. In this review, we explain some problems with narrative biogeography and show how the use of explicit hypotheses is changing understanding of how organisms came to be distributed as they are. Developing synergies between biogeography, ecology, molecular dating and palaeontology are providing novel data and hypothesis-testing opportunities. New approaches are challenging the classic ‘Gondwana’ paradigm and a more complicated history of the Southern Hemisphere is emerging, involving not only general drivers such as continental drift and niche conservatism, but also drowning and re-emergence of landmasses, biotic turnover and long-distance colonization.**

## What is biogeography?

Biogeography is the study of the distribution and evolution of organisms through space and time [1]. New methods have given impetus to the discipline: for example, geographic information systems (GIS) for spatial analysis [2]; Bayesian molecular phylogenetics for dating divergences between lineages [3]; and integrative models for reconstructing distributional change through evolutionary time, using either maximum likelihood [4] or Bayesian inference [5]. Above all, renewed recognition that ecological factors (e.g. climatic tolerance and dispersal limitation) underlie deep historical events (i.e. speciation, extinction and distributional change) [6,7] has rekindled interest in old questions, such as ‘how do ecological factors influence the processes of vicariance and long-distance dispersal and establishment (LDDE)?’ (see Glossary) [6–8]. It has also stimulated new questions, such as ‘what is the role of niche conservatism in large-scale community assembly?’ [8–10]. In the beginning, with Wallace and Darwin, biogeography was an exploration of evolution and it is popular today because, with new methods, it can open windows on the geographical dimensions of speciation. Although hypotheses about ancient ecological processes are not testable by direct observation or experiment, their predictions about present-day biota can potentially be tested. These include predictions about distributional patterns, fossils, likelihoods of dispersal, and the shapes and timing of phylogenies [11].

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## A purely inductive approach (‘pattern before process’) is not science

Unfortunately, biogeography often lacks rigour when it is presented as a geo-historical narrative for a single taxon, commonly as an addendum to a phylogenetic analysis. Biogeography deals with historical events that can neither be observed directly nor manipulated experimentally, and this limitation has been used to justify inductivism; that is, the view that researchers should first observe and analyse the present-day pattern and only then might explanations emerge in terms of historical processes (‘pattern before process’) [12,13]. In a commonly used inductivist approach,

### Glossary

**Area cladogram:** a phylogeny in which the names of the organisms at the tips are replaced by those of the areas in which they occur (e.g. [13,19]).

**Ancestral area reconstruction (AAR):** inference of hypothetical ancestral areas at the internal nodes (and root) of a phylogeny by ‘optimizing’ from known areas at the tips of an area cladogram. Several methods are used for AAR, including parsimony and increasingly complex models using maximum likelihood and Bayesian inference.

**Biotic turnover:** extinction and replacement of floras and faunas in the fossil record, usually driven by global environmental change.

**Crown age:** the age of the most recent common ancestor shared by the extant species of a monophyletic lineage. The crown age of a lineage might be considerably younger than its stem age (Box 3, Figure 1a). See also ‘Stem age’.

**Stem age:** the time when a lineage diverged from its sister group; that is, from the lineage that includes its nearest living relatives. See also ‘Crown age’.

**Long-distance dispersal and establishment (LDDE)\*:** allopatric (geographical) speciation caused by an exceptional dispersal event, establishing a new population on the far side of a barrier that sufficiently limits subsequent gene flow between the parent and daughter populations. See also ‘Vicariance’.

**Niche conservatism:** the notion that major ecological niches are more conserved than expected through evolutionary time is based on the observation from phylogenetic studies that major niche shifts have been relatively rare [9].

**Vicariance\*:** allopatric (geographical) speciation caused by the origination of a barrier within the range of the ancestral species, disrupting gene flow between the now separated subpopulations. See also ‘LDDE’.

**West Wind Drift:** the strongly asymmetrical flow of wind and ocean currents from west to east in the temperate latitudes of the Southern Hemisphere, thought to be responsible for directionally biased LDDE in that hemisphere [19,20].

\*Note that allopatric speciation requires processes in addition to those that cause the disjunction and establishment of disjunct populations. See examples in main text; for example, plant species shared by Tasmania and New Zealand. However, the speciation processes should be similar under either the vicariance or the LDDE model.

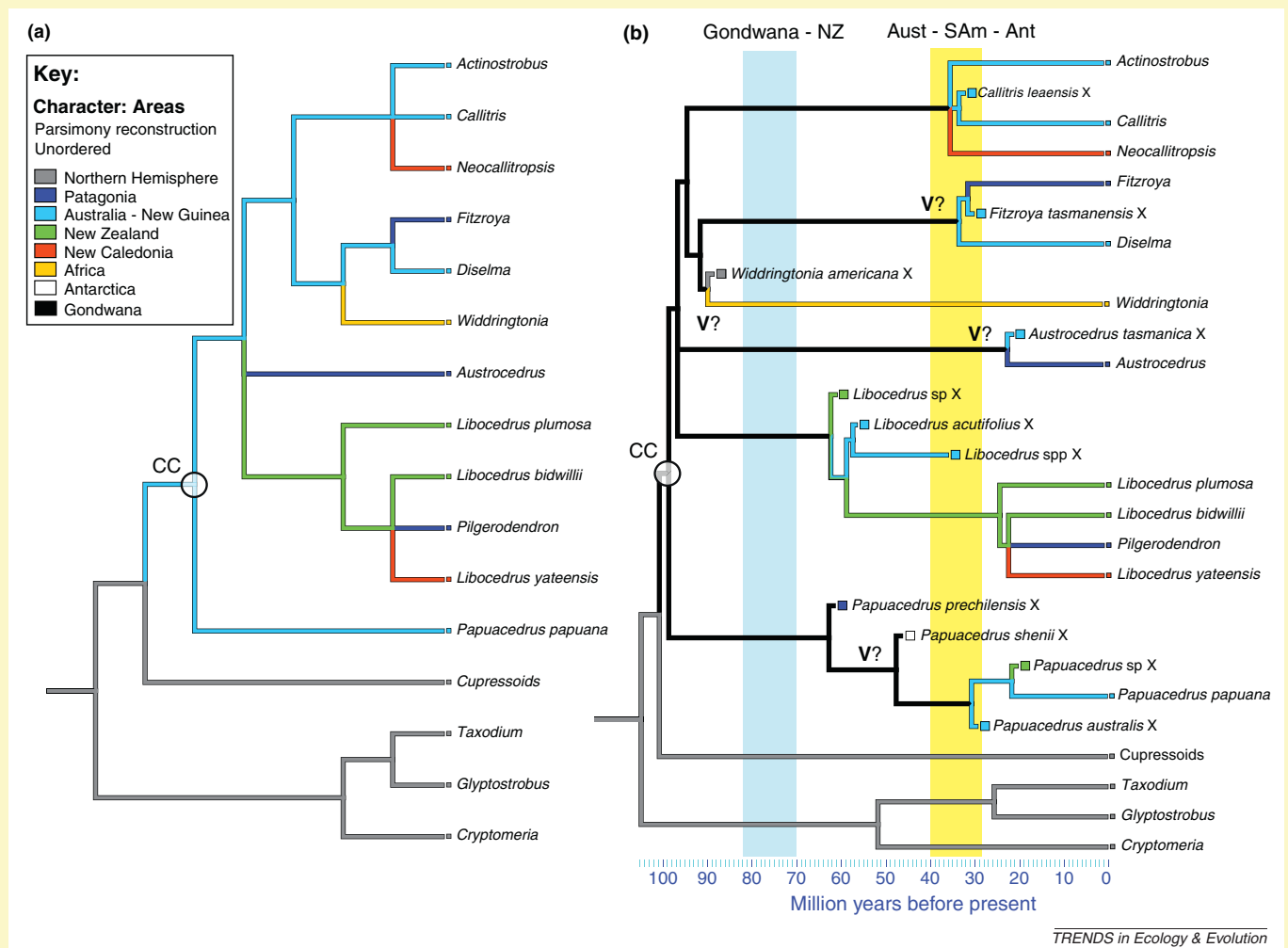
### Box 1. The pattern-first and hypothesis-testing approaches can lead to different conclusions

A common question in biogeography asks ‘what is the geographical origin of taxon A?’ Recent examples include Nilsson *et al.* [65] in respect of marsupials and Brown *et al.* [48] in respect of *Rhododendron* sect. *Vireya*. Here, we illustrate two different approaches to formulating and testing biogeographical hypotheses, using the Southern Hemisphere Callitroid clade of the cypress family (Cupressaceae) as a hypothetical example. Each approach results in a different interpretation of the biogeographical history.

The first is a ‘pattern before process’ approach (Figure 1a), in which the distributions of extant taxa are mapped at the tips of a phylogeny and ancestral areas are reconstructed at internal nodes using any of several methods [14]. Here, both parsimony (mapped in Figure 1a) and maximum likelihood infer that the common ancestor of the Callitroid clade probably originated in Australia and that its descendants subsequently dispersed to New Zealand (green), New Caledonia (red, twice), Patagonia (purple, three times) and South Africa (yellow). However, this commonly used trait-mapping approach fails to consider alternative hypotheses or data that are independent of the tree.

The second approach (Figure 1b) uses the same molecular phylogeny to illustrate how process-based hypothesis testing gives a different conclusion. Fossils can be used to test vicariance versus

dispersal hypotheses by adding extinct lineages and their distributions to the phylogeny (Figure 1b), and by adding a time calibration to the tree. Here, interpretation of fossils indicates that most Callitroid genera were once more widespread across Gondwana but have suffered extensive extinction [56–58]. Knowing this enables one to frame hypotheses of vicariance for some nodes (those with daughter lineages distributed among continents) and assess them using the tests detailed in Box 2. This approach leads, in many cases, to the conclusions that vicariance (nodes labelled V?) cannot be rejected as the cause of divergence. For example, *Fitzroya cupressoides* in Patagonia (extant) probably diverged from its sister *Fitzroya tasmaniensis* in Australia (now extinct) between 30 and 40 mya, about the time when these landmasses separated as East Gondwana broke up (yellow bar). Not all labelled divergences overlap the geological separation bars (e.g. *Papuacedrus*, *Widdringtonia* and *Austrocedrus*) but their confidence intervals probably would, in which case vicariance hypotheses could not be ruled out for these either. (This is a hypothetical example and the relations of fossils have not yet been fully verified by experts. A more rigorous approach to estimating divergence times would also use the fossils to calibrate nodes in a molecular dating analysis; e.g. using BEAST [3].)



**Figure 1.** (a) Ancestral area reconstruction using parsimony to map distributions of cypresses on a phylogeny redrawn from [66] infers an Australian origin for the Callitroid clade followed by dispersal to other Southern Hemisphere landmasses. (b) Adding relationships of fossils (and thus a time calibration) to the phylogeny leads to a failure to reject vicariance hypotheses based on the break up of Gondwana. The blue-shaded bar indicates separation of Zealandia from the remainder of Gondwana and the geological origin of New Zealand [26,59]; the yellow-shaded bar indicates separation of Australia, Antarctica and Patagonia. Extinct taxa are labelled with cross symbols. The most recent common ancestor of the Callitroid clade is labelled ‘CC’. Divergences for which vicariance is not rejected as the cause of the disjunction are labelled ‘V?’.

ancestral areas are reconstructed at internal nodes of the phylogeny; for example, using ancestral area reconstruction (AAR) methods (reviewed in [14,15]), which are sometimes combined with relaxed molecular-clock dating of nodes (Box 1).

Conceptually, AAR does not differ from mapping phenotypic traits ('standard' or 'morphological' characters) onto phylogenies. Geographical distribution is also a trait that can be modelled and, similar to any trait, it can change through time. Thus, standard ancestral trait reconstruction models, based on parsimony, maximum likelihood and Bayesian inference [5,16], have been used in biogeography. Subsequently, complex biogeographical models have been developed to take account of: (i) geological, ecological and geographical factors relevant to distributional change; and (ii) causal links between distributional change (e.g. vicariance or LDDE), speciation and extinction ([4,17,18] and references therein). AAR models differ in their (sometimes unspecified) assumptions about processes, such as whether speciation is constrained to accompany LDDE or whether vicariance is favoured over LDDE [14]. Methods also differ in whether, and to what extent, they enable ancestors to occupy multiple areas (a required assumption for vicariance [14]), and whether they model directional bias in LDDE [19,20]. Ancestral area reconstructions are then typically used to describe a sequence of distributional change through time. Correlates between the inferred distributional changes and 'events', such as continental break up or climate change, are sought and often inferred as causative.

A logical problem with this type of approach, which is not exclusive to biogeography, is that a finite set of observations can be consistent with an almost unlimited set of alternative explanations [1,21–23]. Moreover, 'observations' could be subjective or biased if the observer filters the data through an explanatory theory, even if this process is subconscious [1,21]. Proponents of inductive ('pattern before process') biogeography commonly work from implicit process assumptions, usually of vicariance [22,23]. The inductive approach has been criticised as storytelling and unscientific: alone, it cannot progress beyond being a speculative first attempt to understand the biogeography of a group, because it tends to generate, rather than test, hypotheses [1,13].

Biogeography becomes a science in the Popperian sense when it frames and tests hypotheses [1,13]. Biogeographical knowledge can progress beyond the inductive hypothesis-creation stage by framing restrictive propositions and testing specific predictions that can rule out many of the alternatives [1]. Thus, an untestable question, such as 'where did *Nothofagus* (southern beeches) first evolve?' does not express a specific prediction and could be replaced by a testable hypothesis, such as 'the disjunction between *Nothofagus* sister taxa in Australia and South America was caused by vicariance'. A hypothesis about an unobserved process can be tested if it predicts an observable outcome (e.g. pattern or timing) that contrasts with that from an alternative hypothesis [24]. How biogeographical questions are phrased dictates how they are addressed, and can affect the interpretation of past events (Box 1).

To avoid circularity, it is important to test a hypothesis using data that are independent of those used to frame it in

the first place [23,24]. For example, the hypothesis that the entire terrestrial biota of New Zealand established and diversified after the Oligocene was proposed on the basis of multiple lines of geological evidence that indicate total marine inundation of the landscape before 23 million years ago (mya) [23,25]. This hypothesis can be tested by its prediction that no terrestrial lineage occupied New Zealand and continuously through the Oligocene. The drowning hypothesis would be falsified by the existence in New Zealand of an endemic radiation with a crown age reliably dated to the Oligocene (23–34 mya) or older [23,26]. Phylogenies used for the test should be calibrated using independent data (e.g. from fossils or stratigraphy), rather than the non-independent geological data used to erect the drowning hypothesis.

Here, we discuss some specific approaches to testing hypotheses, using as examples the well-known models of vicariance and dispersal that have been used to explain disjunct distributions. Examples of biogeographical hypotheses and their testable predictions are detailed in Table S1 (supplementary material online).

### Testing alternative hypotheses to explain current disjunct distributions

Vicariance and LDDE are both geographical (allopatry-based) explanations for the process of speciation and, although both probably had a role in the diversification of lineages [8,27], many biogeographers treat them as exclusive alternative models. Vicariance, by definition, results from processes that restrict the dispersal of individuals within the range of a species [6] and this can occur only after the range of a species has already expanded via dispersal. Long-distance dispersal and establishment requires that organisms overcome some barrier to gene flow, but infrequently enough that populations on either side of the barrier (or filter) speciate [19].

The relative contributions of dispersal and vicariance to distributions of organisms in the Southern Hemisphere, where closely related terrestrial species are disjunct across wide oceanic gaps, have been debated extensively. Following the recognition of plate tectonics [28], these distributions have often been explained as arising by vicariance through continental drift [13,29]. Vicariance biogeography under this scenario postulates that, as Gondwana broke up, populations were sundered, isolated on the newly formed landmasses and subsequently diverged to become different species [13,29]. This scenario requires that each species was widespread across much of Gondwana before the break up of the supercontinent. Vicariance has meaning in the evolutionary sense only when it is tied to a divergence event. Thus, continental drift leading to the separation of lineages across oceans is not a cause of vicariance if the lineages were already diverged by the time continental drift separated the landmasses.

The alternative LDDE model for transoceanic disjunctions posits that, driven by rare events (such as storms or tsunamis), organisms have been carried across gaps, such as oceans, that are not normally traversed. The model also allows for cases where propagule dispersal is more frequent but survival and establishment is rare (possibly linked with ecological and genetic factors) [30,31]. With

no (or minimal) gene flow, the separated (allopatric) populations evolve independently and, ultimately, speciate.

### Tests of vicariance

If the pattern and timing of the origin of potential vicariance events are known from geological data, vicariance hypotheses are testable because they make several predictions (Table S1 in Supplementary Material Online). The advent of molecular dating has led to the ability to test the timing of divergences and thus test hypotheses of vicariance (Box 2). Surprisingly, most transoceanic plant disjunctions [8] and many of those in animal taxa [26,32,33] have been determined to be asynchronous or too young to be fully explained by the break up of Gondwana. This applies even in the case of iconic taxa, such as *Nothofagus* [34] and kauri pines (*Agathis*) [35] in New Zealand, ostriches in Africa [36] and primates and rodents in South America [37].

Importantly, divergences can be too old to have been caused by a particular geological event [26,31]: the prediction of timing requires a two-tailed test (Box 2). By this criterion, many of the cases of species-poor lineages that

are presented as evidence of long-term occupancy resulting from vicariance, for example, tuatara in New Zealand and *Amborella* in New Caledonia, fail the test of a vicariance explanation [26].

Another important prediction from a hypothesis of vicariance is that multiple lineages will probably be affected by the origin of the putative barrier [7,29]. Thus, a further prediction is that there should be divergences in multiple taxa either side of that barrier dating to that time [7,38,39]. For example, alternative vicariance hypotheses have been proposed for the middle of the Baja Peninsula, California, putatively owing to either climate change during the Pleistocene or marine incursion during the late Miocene–early Pliocene [38]. These were tested for coincident divergence times across the barrier in multiple animal and plant taxa, with some support found for vicariance at the earlier time in nine taxa [40].

### Are hypotheses of dispersal testable?

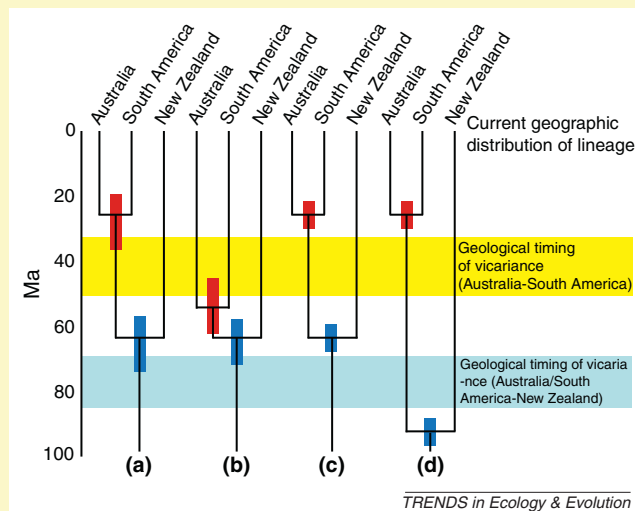
Commonly, dispersal is inferred as the default explanation of a biogeographical disjunction following rejection of a vicariance hypothesis, for example by molecular dating. Therefore, it is important that LDDE hypotheses should be testable using independent evidence. Despite claims that hypotheses of dispersal are not testable [13], careful framing of hypotheses enables some to be tested. As illustrated by the following examples, ecology has an increasing role in testing dispersal hypotheses in historical biogeography.

Example 1. Model-fitting approaches can be used to test dispersal-based hypotheses. For example, Sanmartín *et al.* [20] used parsimony-based tree fitting to test the prediction [19,41,42] that atmospheric and oceanic West Wind Drift should cause an easterly bias in plant dispersals in the Southern Hemisphere. Inferred LDDE events in 23 phylogenies were significantly asymmetrical in the predicted direction, rejecting the null hypothesis of equal rates of inferred dispersal in both directions, as determined from randomizations.

Example 2. Stepping-stone dispersal routes have often been inferred to explain what, for some, might be seemingly impossible LDDE events across extreme barriers. This approach has been especially adopted for terrestrial taxa that are disjunct across oceans, such as between Australia, New Zealand and New Caledonia [43,44], Antarctica and Africa via the Kerguelen Plateau [36] and between Africa and Madagascar [32]. However, stepping-stone routes might be even more problematic than a single jump across a wider gap, because a stepping-stone hypothesis assumes that an intermediate, reproducing population was large enough and existed long enough to produce a ‘propagule (or migrant) pressure’ [30] sufficient to colonize the next land-mass along the chain. For example, it has been suggested that a single extreme LDDE event could be more probable than multiple shorter LDDE (stepping-stone model) events. Long-distance seed ‘dispersal kernels’ (i.e. probability distributions of LDDE) appear to be ‘fat tailed’ [45,46]; that is, extreme LDDE is not much less probable than LDDE over much shorter distances. This is partly because of stochasticity and partly because of infrequent atypical processes (e.g. cyclones and tsunamis) [45]. Given that probabilities multiply in a chain of independent

#### Box 2. Tests of vicariance are two-tailed

Divergence times in molecular phylogenies can be used to test hypotheses of vicariance [27]. Vicariance hypotheses predict that the divergence time between taxa on either side of a barrier should coincide with the timing of the origin of that barrier. The test is two tailed. Vicariance is rejected if the divergence between the taxa is too young (post-dates the origin of the barrier) or too old (pre-dates origin of barrier) and, thus, the barrier could not have caused the divergence (Figure 1). The test of vicariance is explicit as it addresses a specific divergence (node) in the phylogeny, which is hypothesized to be caused by the origin of a particular barrier. A rejection of one vicariance event does not equate to ‘vicariance does not explain the distribution of this taxon’. It can reject only the hypothesis that ‘vicariance event X explains node Y’.



**Figure 1.** Four scenarios showing different timing of divergences between three lineages. Each phylogeny enables the testing of two hypotheses of vicariance: one between South America and Australia (with red confidence interval bars) and another between Australia + South America and New Zealand (with dark-blue confidence interval bars). All vicariance hypotheses cannot be rejected in (a) and (b) because the divergence-time error bar overlaps the relevant geological time bar in each case. In (c) and (d), all vicariance hypotheses are rejected because the respective error bars and divergence time bars do not overlap.

events, a single, long LDDE is likely to be more probable than are multiple, shorter steps. Using the hypothetical dispersal kernel of Nathan ([45]: Figure 2, corrected version, published 17 October 2006), the probability of a single seed arrival over 500 km is  $P = 10^{-16}$  and that of a single seed arrival over 1000 km is  $P = 10^{-18}$ . However, the probability of two consecutive jumps over 500 km, with the second contingent on the first, is  $P = (10^{-16})^2 = 10^{-32}$ ; that is, more improbable than the single jump over 1000 km.

Example 3. Ecological parameters, such as the above dispersal probability kernels, can be included in model-based tests of alternative dispersal hypotheses [4,18]. This approach integrates ‘historical’ and ‘ecological’ biogeography, two domains once thought to be independent because of their differing time scales and treatment of evolution (ancient and evolutionary versus recent and non-evolutionary, respectively) [47]. Webb and Ree [18] compared two alternative hypotheses from [48] to explain the occurrence of species of *Rhododendron* sect. *Vireya* on both sides of Wallace’s Line, a putatively ancient division between the biotas of South-east Asia and Australasia, caused by plate tectonics [49]. Webb and Ree used SHIBA [18], a program that simulates lineage movement on a changing historical landscape, as determined from geological data, and makes probabilistic estimates of ancestral ranges. Their model also included ecological parameters from the theory of island biogeography [50], namely survival versus area, and dispersal versus distance. The authors then used this model to test contrasting hypotheses about the age of the radiation of *Rhododendron* sect. *Vireya* in the island archipelago of Malesia by comparing the likelihoods of biogeographical reconstructions using the alternative root ages (55 mya vs 12 mya). Their test determined that a single LDDE event at 55 mya was more probable than shorter stepping-stone dispersals through islands that came into existence more recently.

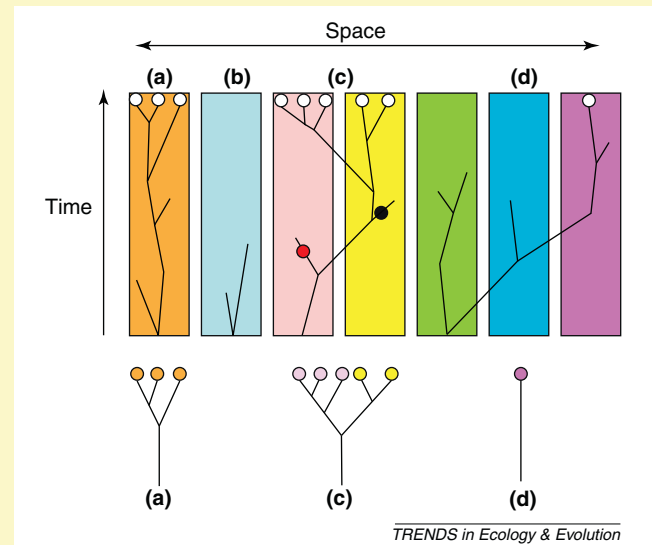
### The problem of extinction

Extinction has long been acknowledged as a key determinant of observable biogeographical patterns, but is often considered intractable and ignored [13]. One reason is that it is difficult to reconstruct (Box 3) unless the fossil record provides compelling evidence of the former presence of taxa in areas where they are no longer found [51]. The reverse, lack of fossil evidence of a former presence of a taxon in a given area, should not be accepted *prima facie* as evidence that it was always absent, given the stochastic nature of the fossil record (Box 3, Figure 1b).

Despite the difficulties, it is essential to consider extinction in testing biogeographical hypotheses because it can result in false reconstructions that appear to be well supported (Box 3). Biotic turnover has probably been overlooked because fossils of extinct lineages have been misassigned to younger, related lineages that have immigrated more recently, giving a false impression of long-term occupancy of a region by the original lineage (Box 3, Figure 1c). For example, in New Zealand, evidence is emerging of previously overlooked floristic turnover through the Cenozoic [52], for example in *Nothofagus* [34], *Ericaceae* [53] and *Agathis* [35].

### Box 3. Extinction needs to be considered in hypothesis formulation

No current method of AAR using phylogenies can reconstruct as ancestral an area that has not been observed in present-day species and, consequently, has not been included in the analysis, *cf.* [67]. Only the fossil record (if available) can provide evidence of former occurrences of taxa in areas where they are now extinct (e.g. [51,64]). Extinction can mislead by differentially erasing any kind of biogeographical pattern, including dispersal pattern, and it can remove evidence from either a particular time period or a particular region.



**Figure 1.** Biogeographical histories of hypothetical lineages. Open circles represent living taxa, filled circles indicate fossil taxa, black lines indicate actual phylogenetic relationships and coloured bars indicate hypothetical locations through time. As biogeographical history is ‘known’, one can intuit that: (a) the age of a crown group does not equate to the age of the lineage in a particular area; (b) current absence of a lineage does not equate to past absence; (c) current presence of a lineage (pink area) does not equate to continuous past presence; and (d) relict taxa or living fossils do not necessarily indicate long occupation of an area, but might reflect high levels of extinction. Using a phylogeny from sequence data for extant taxa (at bottom of figure), rate modelling and AAR, a biogeographer could infer a common ancestor for each of (c) and (d) but could not infer where the ancestor existed through time. Inclusion of one available dated fossil (solid-black circle) could result in correct time calibration and inference of ancestral locality. Alternatively, inclusion of a different dated fossil (solid-red circle) could lead to incorrect inferences of both the location and age of the common ancestor. Thus, uncertainty about the placement of fossils yields uncertainty about biogeographical inference, regardless of the sophistication of the phylogenetic tools.

Thus, the fossil record, and the probable biases and/or uncertainty it implies, should be considered as far as possible in biogeographical analysis [51]. For example, some extant ‘Gondwanan’ groups have an unequivocal, even extensive, ancient fossil record in the Northern Hemisphere, where they have apparently gone extinct (*cf.* Box 3, Figure 1d); for example, marsupials [54], Rhynchocephalia (tuatara) [55], southern conifers such as *Araucariaceae* and many *Podocarpaceae* [56]. Similarly, there are fossils of several genera of the cypress family (*Cupressaceae*) from Southern Hemisphere areas where they are now extinct [56–58]; Box 1 illustrates how incorporating this fossil evidence into hypotheses can change how researchers assess the biogeographical history of the family.

Geographically restricted taxa that are species poor and sister to a species-rich lineage (often referred to as ‘relicts’)

tend to invite speculation about their origins and biogeography. Examples include *Ginkgo* in China, tuatara and *Agathis* in New Zealand, and the endemic shrub *Amborella* in New Caledonia. However, extant taxa indicate persistence in time only, not in space (Box 3, Figure Id), and 'relict' lineages cannot be assumed to have occupied the present space throughout the existence of the lineage. Such lineages have probably been subject to considerable extinction and, in the absence of additional data, are essentially uninformative about biogeographical history, presenting little scope for erecting testable hypotheses. Even though the above taxa (except *Amborella*) have an excellent ancient fossil record and have been geographically widespread in the past, their restriction to a single surviving species in a localized area is shrouded in mystery.

### Conclusions and the way ahead

Understanding of how lineages became distributed as they are has changed dramatically because biogeographers are taking a more focused, critical approach. Sweeping questions such as 'where did cypresses evolve?' are being replaced with focused, testable hypotheses, such as 'the ancestor of the extant cypress species of *Libocedrus* in New Zealand arrived by LDDE after the Oligocene drowning'. Consequently, it has been learned that the geographical evolution of biota has been driven by a greater diversity of processes with a more complex history than under a simple vicariance (or dispersal) paradigm. For example, tests of predictions from geology and ecology have shown that, to a large degree, New Zealand and New Caledonia resemble 'oceanic' islands with young, immigrant biota, rather than 'continental' islands with relictual 'Gondwanan' biota [26,59,60].

Future biogeographical models will become more complex, sophisticated and realistic, as they incorporate estimates of ecological parameters, such as dispersal kernels [7,61]. Models can be used to test hypotheses by varying the parameter under question while holding others constant, within a statistical framework [7,11,18]. However, models require validation with independent empirical data on crucially important parameter values [19,23] and these are difficult to obtain, especially in an historical context. Important parameters to include are the shape of the tail of the LDDE distribution and the distances beyond which reduced gene flow leads to divergence. Such parameters are difficult to quantify and are likely to be species or ecology specific. Current historical models use parameter values that are either best guesses, or worse, are estimated from phylogenies and, thus, not independent of them. Increasingly, geo-referenced ecological and climatic parameters are being integrated into tests of alternative spatial models of community diversification and distribution [7]. Current climatic models are well validated and implemented in GIS at fine geographical and seasonal scales. Extending such models to ancient time periods is challenging, partly because past climates are commonly reconstructed using fossil evidence, so using the reconstructions for testing biogeographical hypotheses could be circular.

The fossil record is emerging again as being crucially important in biogeography (e.g. [51]), and we have reiter-

ated here, with examples, that ignorance of the role of extinction can lead to misinterpretation. Auspiciously, new collaborations between palaeontologists and molecular systematists [8,35,53,62,63] are leading to reinterpretation of fossils, resulting in improvement of the phylogenetic placement of calibration points and more reliable divergence time estimates. In addition, ecological parameters estimated from extant organisms can help explain distributional changes when compared with the fossil record. For example, ecophysiological tolerances were measured in living conifer genera, some of which are extinct in Australia but have a fossil record there [64]. It was found that, unlike the extant Australian genera, those that are extinct probably had moisture tolerances that fell outside the current range of climates in Australia [64]. This type of integrative approach is resulting in more critical tests of biogeographical hypotheses and is changing the current view of the history of the biota of the world.

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### Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.tree.2010.11.005.

### References

- Ball, I.R. (1976) Nature and formulation of biogeographical hypotheses. *Syst. Zool.* 24, 407–430
- Rosauer, D. *et al.* (2009) Phylogenetic endemism: a new approach for identifying geographical concentrations of evolutionary history. *Mol. Ecol.* 18, 4061–4072
- Drummond, A.J. *et al.* (2006) Relaxed phylogenetics and dating with confidence. *PLoS Biol.* 4, e88
- Ree, R.H. and Smith, S.A. (2008) Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Syst. Biol.* 57, 4–14
- Lemey, P. *et al.* (2009) Bayesian phylogeography finds its roots. *PLoS Comput. Biol.* 5, 16
- Wiens, J.J. and Donoghue, M.J. (2004) Historical biogeography, ecology and species richness. *Trends Ecol. Evol.* 19, 639–644
- Riddle, B.R. *et al.* (2008) The role of molecular genetics in sculpting the future of integrative biogeography. *Prog. Phys. Geogr.* 32, 173–202
- Crisp, M.D. *et al.* (2009) Phylogenetic biome conservatism on a global scale. *Nature* 458, 754–756
- Donoghue, M.J. (2008) A phylogenetic perspective on the distribution of plant diversity. *Proc. Natl. Acad. Sci. U. S. A.* 105, 11549–11555
- Wiens, J.J. *et al.* (2010) Niche conservatism as an emerging principle in ecology and conservation biology. *Ecol. Lett.* 13, 1310–1324
- Pigot, A.L. *et al.* (2010) The shape and temporal dynamics of phylogenetic trees arising from geographic speciation. *Syst. Biol.* 59, 660–673
- Andersson, L. (1996) An ontological dilemma: epistemology and methodology of historical biogeography. *J. Biogeogr.* 23, 269–277
- Humphries, C.J. (2004) From dispersal to geographic congruence: comments on cladistic biogeography in the twentieth century. In *Milestones in Systematics* (Williams, D.M. and Forey, P.L., eds), pp. 225–260, CRC Press
- Lamm, K.S. and Redelings, B.D. (2009) Reconstructing ancestral ranges in historical biogeography: properties and prospects. *J. Syst. Evol.* 47, 369–382
- Kodandaramaiah, U. (2010) Use of dispersal-vicariance analysis in biogeography; a critique. *J. Biogeogr.* 37, 3–11

- 16 Lewis, P.O. (2001) A likelihood approach to estimating phylogeny from discrete morphological character data. *Syst. Biol.* 50, 913–925
- 17 Sanmartín, I. *et al.* (2008) Inferring dispersal: a Bayesian approach to phylogeny-based island biogeography, with special reference to the Canary Islands. *J. Biogeogr.* 35, 428–449
- 18 Webb, C.O. and Ree, R.H. Historical biogeography inference in Malaysia. In *Biotic evolution and environmental change in Southeast Asia* (Gower, D. and Ruber, L., eds.), Cambridge University Press (in press)
- 19 Cook, L.G. and Crisp, M.D. (2005) Directional asymmetry of long-distance dispersal and colonisation could mislead reconstructions of biogeography. *J. Biogeogr.* 32, 741–754
- 20 Sanmartín, I. *et al.* (2007) West Wind Drift revisited: testing for directional dispersal in the Southern Hemisphere using event-based tree fitting. *J. Biogeogr.* 34, 398–416
- 21 Popper, K.R. (1959) *The Logic of Scientific Discovery*, Hutchinson
- 22 McDowall, R.M. (2004) What biogeography is: a place for process. *J. Biogeogr.* 31, 345–351
- 23 Waters, J.M. and Craw, D. (2006) Goodbye Gondwana? New Zealand biogeography, geology, and the problem of circularity. *Syst. Biol.* 55, 351–356
- 24 Penny, D. and Phillips, M.J. (2004) The rise of birds and mammals: are microevolutionary processes sufficient for macroevolution? *Trends Ecol. Evol.* 19, 516–522
- 25 Landis, C.A. *et al.* (2008) The Waipounamu Erosion Surface: questioning the antiquity of the New Zealand land surface and terrestrial fauna and flora. *Geol. Mag.* 145, 173–197
- 26 Goldberg, J. *et al.* (2008) Evolution of New Zealand's terrestrial fauna: a review of molecular evidence. *Philos. Trans. R. Soc. B, Biol. Sci.* 363, 3319–3334
- 27 Donoghue, M.J. and Moore, B.R. (2003) Toward an integrative historical biogeography. *Integr. Comp. Biol.* 43, 261–270
- 28 Hammond, A.L. (1971) Plate tectonics: the geophysics of the Earth's surface. *Science* 173, 40–41
- 29 Rosen, D.E. (1978) Vicariant patterns and historical explanation in biogeography. *Syst. Zool.* 27, 159–188
- 30 Simberloff, D. (2009) The role of propagule pressure in biological invasions. *Annu. Rev. Ecol. Evol. Syst.* 40, 81–102
- 31 Trewick, S.A. and Gibb, G.C. (2010) Vicars, tramps and assembly of the New Zealand avifauna: a review of molecular phylogenetic evidence. *Ibis* 152, 226–253
- 32 Poux, C. *et al.* (2005) Asynchronous colonization of Madagascar by the four endemic clades of primates, tenrecs, carnivores, and rodents as inferred from nuclear genes. *Syst. Biol.* 54, 719–730
- 33 Wallis, G.P. and Trewick, S.A. (2009) New Zealand phylogeography: evolution on a small continent. *Mol. Ecol.* 18, 3548–3580
- 34 Cook, L.G. and Crisp, M.D. (2005) Not so ancient: the extant crown group of *Nothofagus* represents a post-Gondwanan radiation. *Proc. R. Soc. B, Biol. Sci.* 272, 2535–2544
- 35 Biffin, E. *et al.* (2010) Did kauri (*Agathis*: Araucariaceae) really survive the Oligocene drowning of New Zealand? *Syst. Biol.* 59, 594–610
- 36 Phillips, M.J. *et al.* (2010) Tinamous and moa flock together: mitochondrial genome sequence analysis reveals independent losses of flight among ratites. *Syst. Biol.* 59, 90–107
- 37 Poux, C. *et al.* (2006) Arrival and diversification of caviomorph rodents and platyrrhine primates in South America. *Syst. Biol.* 55, 228–244
- 38 Lindell, J. *et al.* (2006) Deep genealogies and the mid-peninsular seaway of Baja California. *J. Biogeogr.* 33, 1327–1331
- 39 Crisp, M.D. and Cook, L.G. (2007) A congruent molecular signature of vicariance across multiple plant lineages. *Mol. Phylogenet. Evol.* 43, 1106–1117
- 40 Riddle, B.R. and Hafner, D.J. (2006) A step-wise approach to integrating phylogeographic and phylogenetic biogeographic perspectives on the history of a core North American warm deserts biota. *J. Arid Envir.* 66, 435–461
- 41 Waters, J.M. and Roy, M.S. (2004) Out of Africa: the slow train to Australasia. *Syst. Biol.* 53, 18–24
- 42 Muñoz, J. *et al.* (2004) Wind as a long-distance dispersal vehicle in the Southern Hemisphere. *Science* 304, 1144–1147
- 43 Ladiges, P.Y. and Cantrill, D. (2007) New Caledonia–Australian connections: biogeographic patterns and geology. *Aust. Syst. Bot.* 20, 383–389
- 44 Heads, M. (2008) Panbiogeography of New Caledonia, south-west Pacific: basal angiosperms on basement terranes, ultramafic endemics inherited from volcanic island arcs and old taxa endemic to young islands. *J. Biogeogr.* 35, 2153–2175
- 45 Nathan, R. (2006) Long-distance dispersal of plants. *Science* 313, 786–788
- 46 Hardy, O.J. (2009) How fat is the tail? *Heredity* 103, 437–438
- 47 Rosen, B.R. (1988) Biogeographic patterns: a perceptual overview. In *Analytical Biogeography* (Myers, A.A. and Giller, P.S., eds), pp. 23–55, Chapman and Hall
- 48 Brown, G.K. *et al.* (2006) Historical biogeography of *Rhododendron* section *Vireya* and the Malesian Archipelago. *J. Biogeogr.* 33, 1929–1944
- 49 Whitmore, T.C. (1982) Wallace's Line: a result of plate tectonics. *Ann. Mo. Bot. Gard.* 69, 668–675
- 50 McArthur, R.H. and Wilson, E.O. (1967) *The Theory of Island Biogeography*, Princeton University Press
- 51 Quental, T.B. and Marshall, C.R. (2010) Diversity dynamics: molecular phylogenies need the fossil record. *Trends Ecol. Evol.* 25, 434–441
- 52 Pole, M.S. (2001) Can long-distance dispersal be inferred from the New Zealand plant fossil record? *Aust. J. Bot.* 49, 357–366
- 53 Jordan, G.J. *et al.* (2010) Fossil Ericaceae from New Zealand: deconstructing the use of fossil evidence in historical biogeography. *Am. J. Bot.* 97, 59–70
- 54 Vullo, R. *et al.* (2009) The oldest modern therian mammal from Europe and its bearing on stem marsupial paleobiogeography. *Proc. Natl Acad. Sci. U. S. A.* 106, 19910–19915
- 55 Jones, M.E. *et al.* (2009) A sphenodontine (Rhynchocephalia) from the Miocene of New Zealand and palaeobiogeography of the tuatara (*Sphenodon*). *Proc. R. Soc. B, Biol. Sci.* 276, 1385–1390
- 56 Hill, R.S. and Brodribb, T.J. (1999) Southern conifers in time and space. *Aust. J. Bot.* 47, 639–696
- 57 Wilf, P. *et al.* (2009) *Papuacedrus* (Cupressaceae) in Eocene Patagonia: a new fossil link to Australasian rainforests. *Am. J. Bot.* 96, 2031–2047
- 58 Paull, R. and Hill, R.S. (2010) Early Oligocene *Callitris* and *Fitzroya* (Cupressaceae) from Tasmania. *Am. J. Bot.* 97, 809–820
- 59 Trewick, S.A. *et al.* (2007) Hello New Zealand. *J. Biogeogr.* 34, 1–6
- 60 Grandcolas, P. *et al.* (2008) New Caledonia: a very old Darwinian island? *Philos. Trans. R. Soc. B, Biol. Sci.* 363, 3309–3317
- 61 Nathan, R. *et al.* (2008) Mechanisms of long-distance seed dispersal. *Trends Ecol. Evol.* 23, 638–647
- 62 Ho, S.Y.W. and Phillips, M.J. (2009) Accounting for calibration uncertainty in phylogenetic estimation of evolutionary divergence times. *Syst. Biol.* 58, 367–380
- 63 Sauquet, H. *et al.* (2009) Contrasted patterns of hyperdiversification in Mediterranean hotspots. *Proc. Natl Acad. Sci. U. S. A.* 106, 221–225
- 64 Hill, R.S. (2004) Origins of the southeastern Australian vegetation. *Philos. Trans. R. Soc. B, Biol. Sci.* 359, 1537–1549
- 65 Nilsson, M.A. *et al.* (2010) Tracking marsupial evolution using archaic genomic retroposon insertions. *PLoS Biol.* 8, e1000436
- 66 Gadek, P.A. *et al.* (2000) Relationships within Cupressaceae *sensu lato*: a combined morphological and molecular approach. *Am. J. Bot.* 87, 1044–1057
- 67 Oakley, T.H. and Cunningham, C.W. (2000) Independent contrasts succeed where ancestor reconstruction fails in a known bacteriophage phylogeny. *Evolution* 54, 397–405