



Directional asymmetry of long-distance dispersal and colonization could mislead reconstructions of biogeography

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ABSTRACT

Aim Phylogenies are increasingly being used to attempt to answer biogeographical questions. However, a reliance on tree topology alone has emerged without consideration of earth processes or the biology of the organisms in question. Most ancestral-state optimization methods have inherent problems, including failure to take account of asymmetry, such as unequal probabilities of losses and gains, and the lack of use of independent cost estimates. Here we discuss what we perceive as shortcomings in most current tree-based biogeography interpretation methods and show that consideration of processes and their likelihoods can turn the conventional biogeographical interpretation on its head.

Location Southern hemisphere focus but applicable world-wide.

Methods The logic of existing methods is reviewed with respect to their adequacy in modelling processes such as geographical mode of speciation and likelihood of dispersal, including directional bias. Published reconstructions of dispersal of three plant taxa between Australia and New Zealand were re-analysed using standard parsimony and maximum likelihood (ML) methods with rate matrices to model expected asymmetry of dispersal.

Results Few studies to date incorporate asymmetric dispersal rate matrices or question the simplistic assumption of equal costs. Even when they do, cost matrices typically are not derived independently of tree topology. Asymmetrical dispersal between Australia and New Zealand could be reconstructed using parsimony but not with ML.

Main conclusions The inadequacy of current models has important consequences for our interpretation of southern hemisphere biogeography, particularly in relation to dispersal. For example, if repeated directional dispersals and colonization in the direction of prevailing winds have occurred, with intervening periods of speciation, then there is no need to infer dispersals against those winds. Failure to take account of directionality and other biases in reconstruction methods has implications beyond the simple misinterpretation of the biogeography of a taxonomic group, such as calibration of molecular clocks, the dating of vicariance events, and the prioritization of areas for conservation.

Keywords

Ancestral areas, Antarctic Circumpolar Current, Australia, directional dispersal, maximum likelihood, maximum parsimony, New Zealand, southern hemisphere, trait optimization, West-wind Drift.

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INTRODUCTION

It is commonly accepted that vicariance and long-distance dispersal (LDD) have both contributed to the current

distributions of organisms (Raven, 1973; Wardle, 1978; McDowall, 2004; Thorne, 2004). Even taxa that appear to be poor dispersers have biogeographical patterns that require an inference of dispersal (e.g. amphibians, Vences *et al.*, 2004;

ratites, Cooper *et al.*, 2001; Haddrath & Baker, 2001; hebes, Wagstaff *et al.*, 2002; *Scaevola*, Howarth *et al.*, 2003). Examples also include taxa, such as *Nothofagus*, where the recent accepted paradigm had been one of Gondwanan vicariance (Craw, 1989; Linder & Crisp, 1995; Swenson *et al.*, 2001).

Repeated large-scale biogeographical patterns that are ascribable to LDD indicate that LDD can be directional (Wardle, 1978; McDowall, 2002; Les *et al.*, 2003; Muñoz *et al.*, 2004; Sanmartín & Ronquist, 2004), despite claims by some authors (e.g. Croizat *et al.*, 1974; Nelson & Platnick, 1981; Craw, 1982; Humphries, 2001; McCarthy, 2003) that LDD is inherently stochastic. Although successful LDD and establishment (hereafter referred to as long-distance dispersal and colonization; LDDC) are conditional on variables such as the dispersability of the organism or its propagules, favourable environmental conditions for dispersal and a suitable habitat for establishment, numerous processes involved in dispersal have a strong directional component.

Directional processes include dispersal from continental landmasses onto newly created islands (Bush & Whittaker, 1991; Wagner & Funk, 1995; Nepokroeff *et al.*, 2003), down river systems (e.g. Campbell *et al.*, 2002; Levine, 2003) and, importantly for global-scale patterns, with prevailing winds (e.g. Pedgley, 1982; Greathead, 1990; Levin *et al.*, 2003) or ocean currents (e.g. Wares *et al.*, 2001; Calsbeek & Smith, 2003; Gaines *et al.*, 2003). Additionally, animal-assisted dispersal, such as by birds, might also be directional (e.g. Wardle, 1978; Wenny & Levey, 1998).

Wind and ocean currents are probably the two major abiotic processes that might lead to congruent LDDC patterns across multiple taxa (e.g. Raven, 1973; Wardle, 1978; Gaines *et al.*, 2003; McDowall, 2004; Muñoz *et al.*, 2004). In the Southern Hemisphere, for example, currents are dominated by the Antarctic Circumpolar Current (ACC) and West-wind Drift (WWD) (Bowler, 1982; Colls & Whitaker, 2001) which were initiated after the rifting of South America and Australia from Antarctica *c.* 38 Ma (Veevers *et al.*, 1991). These currents may be responsible for the close taxonomic affinities between southern hemisphere localities that are in conflict with conventional continental drift patterns (e.g. Raven, 1973; Waters *et al.*, 2000a; McDowall, 2002; Muñoz *et al.*, 2004; Sanmartín & Ronquist, 2004).

The westerly wind flow is thought to be responsible for strong affinities between the New Zealand and Australian flora, with some of the New Zealand flora being derived from propagules blown east across the Tasman Sea from Australia, currently a distance of *c.* 2000 km (Raven, 1973; Wardle, 1978; Macphail, 1997; Jordan, 2001; Pole, 2001). Shared extant species across this gap suggest that the process is ongoing, although not universal, and a number of traits apparently influence the likelihood of success (Wardle, 1978; Jordan, 2001; McGlone *et al.*, 2001). For example, populations with very light, wind-dispersed spores, such as ferns, appear more likely to maintain genetic contact over large oceanic gaps and remain conspecific over long periods (Ranker *et al.*, 1994; Wolf *et al.*, 2001). In a phylogenetic context, this results in a sister relationship between

Australia and New Zealand (e.g. *Nothofagus*, Linder & Crisp, 1995), in contrast to the conventional vicariance scenario where New Zealand is sister to Australia + South America. Similarly, ocean currents also appear to play a role in dispersal between Australia and New Zealand. For example, sister relationships among some galaxiids probably reflect relatively recent dispersal between the two regions, possibly on an older background of Gondwanan vicariance (Waters *et al.*, 2000a; McDowall, 2002).

If directional LDDC can lead to congruent patterns across taxa (e.g. Muñoz *et al.*, 2004; Sanmartín & Ronquist, 2004), then multiple occurrences of directional LDDC within a taxon must also be a possibility. That is, if there are repeated patterns across distantly related taxa, why not among closely related taxa? When dispersal is very common, the gene pools of the populations either side of the semipermeable barrier remain in contact and both populations will remain conspecific. However, if there is no further dispersal between the two populations after establishment then, over time, they will both diverge and become separate species (allopatric speciation).

The possible role of repeated directional dispersal and its effect on phylogeny-based reconstructions has been largely neglected. Directionality has significant implications for biogeographical reconstructions derived from phylogenies of taxa that span areas where LDDC is likely to have been directional. By not considering all alternatives, reconstructions may appear more decisive than is perhaps warranted.

INTERPRETING TREES FOR BIOGEOGRAPHY

Most biogeographical studies typically substitute the terminal names of a species or gene tree with the geographical areas of each taxon to produce a taxon–area phylogeny. If a species tree is used, each node of the phylogeny represents a speciation event. Speciation falls into two main categories – allopatric (speciation in geographical isolation) and sympatric (reproductive isolation arising despite individuals' continuously having an opportunity to interbreed). Allopatric speciation is probably more common than sympatric speciation (e.g. Barraclough & Nee, 2001; Turelli *et al.*, 2001) and, to date, there are few examples where sympatric speciation is supported empirically. Interpretation of causes of the speciation events, in the context of tree topology, is used to generate or discriminate among alternative biogeographical hypotheses. In a phylogeny of organisms, taxa diverging at a terminal node (i.e. 'twigs') are typically interpreted as 'the most derived' or 'most recently diverged' taxa (e.g. taxa *A* and *D* in Fig. 1). In terms of biogeography, the equivalent would be 'most recent dispersal to' or 'most recent vicariance event' (Mast & Givnish, 2002; Winkworth *et al.*, 2002a).

Inference of ancestral areas using a taxon–area phylogeny typically depends on maximum parsimony (Bremer, 1992; Maddison & Maddison, 1992; Ronquist, 2003), maximum likelihood (ML) (Cunningham *et al.*, 1998; Cunningham, 1999; Mooers & Schluter, 1999; Pagel, 1999a; Lutzoni *et al.*, 2001) or, more recently, Bayesian (Huelsenbeck & Bollback, 2001; Pagel *et al.*, 2004; Ronquist, 2004) approaches to reconstruction of ancestral states at internal nodes of a tree.

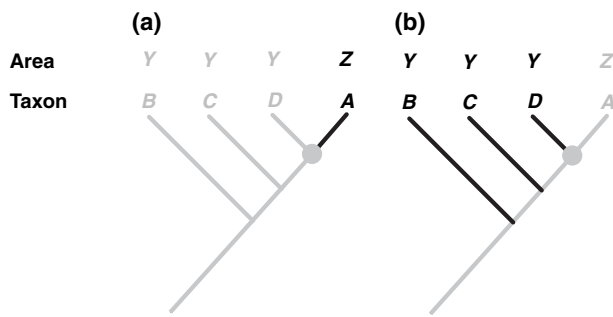


Figure 1 Contrasting interpretations of an area. Grey indicates the source population through time and black indicates dispersed populations. (a) Fitch parsimony explains only the terminal node, by a jump dispersal from area Y resulting in a new species (A) in area Z. Vicariance explains the same node as a split between areas Y and Z, resulting in two new species, respectively D and A. Neither interpretation explains the earlier, apparently sympatric speciation events leading to species B and C in area Y. Therefore, these events are not costed by vicariance or Fitch models. (b) Repeated jump dispersals into area Y from a source population (A) in Z give rise to species B–D, so that species A (and its area Z) is placed at a terminal node by cladistic analysis. This interpretation explains all nodes and events and, although it may seem unparsimonious compared with Fitch or vicariance models, its overall cost is equivalent.

Parsimony

Fitch optimization (equally weighted parsimony) is a commonly used method (e.g. Enghoff, 1995; Andersson & Chase, 2001; Manos & Stanford, 2001; Lieberman, 2002) that, in effect, models dispersal and allopatric speciation (Ronquist, 2003). Only dispersal events are counted and, whilst sympatric speciation is allowed, it is not counted in the parsimony sum (Ronquist, 2003). This involves an *a priori* assumption that is applied across the tree and takes no account of differences among taxa, such as mode of speciation. In Fig. 1, Fitch parsimony explains only the terminal node, by long-distance dispersal from area Y resulting in a new species (A) in area Z. This leads to the conclusion that a population in area Y was the source and that dispersal occurred only once – at the terminal grey node (Fig. 1a). It is assumed that dispersal occurred at the time of this speciation event, and in the direction of the single nested area (Z).

Subtree analysis (Nelson & Ladiges, 1996; Ebach & Humphries, 2002) uses an event-based approach that explicitly favours vicariance over dispersal (Page, 1994; Nelson & Ladiges, 2001; Ronquist, 2003). Using this method, the final speciation event leading to A and D (Fig. 1) would be treated as a vicariance event between areas Z and Y, whereas taxa B and C, also occurring in Y, would be considered paralogous (relative to D) and discarded from further consideration.

Both Fitch and Subtree Analysis are intuitively unsatisfactory because they fail to explain the number of species in the paraphyletic residual in area Y (B–D, Fig. 1).

All nodes are taken into account in a process-based approach to biogeography (Ronquist, 1994, 1998, 2003), such as DIVA, which uses parsimony to choose between different kinds of

events, such as vicariance, dispersal, sympatric speciation (duplication) and extinction, having varying probabilities (Ronquist, 1998; Sanmartín & Ronquist, 2004). DIVA uses a cost matrix to assign a cost to each event type and minimizes the total cost of optimizing areas over the tree (Ronquist, 1997). Speciation by vicariance is considered the null expectation and is given zero cost. Sympatric speciation is also given zero cost. Extinction and dispersal each have unit cost. Therefore, DIVA tends to favour vicariance reconstructions over dispersal. In Fig. 1, DIVA infers a dispersal of the ancestor of D + A into area Z (cost = 1) followed by vicariance (cost = 0) (cf. Ronquist, 1997, Fig. 3a). The user of DIVA may choose to restrict the breadth of possible ancestral distributions to fewer than the sum of descendent areas, and that may be a single area. A broad ancestral distribution would be more consistent with a history of vicariance, and a narrow one with a history of dispersal.

Maximum likelihood

Maximum likelihood modelling of the evolution of traits on trees has several advantages over parsimony (Pagel, 1994, 1999b; Cunningham, 1999; Mooers & Schluter, 1999; Nielsen, 2002) and has been used to estimate ancestral areas (e.g. Nepokroeff *et al.*, 2003). Whereas parsimony reconstructs a single state at each node, ML can indicate the probabilities of alternative states. If change is highly probable relative to branch length, then a basic assumption of parsimony is violated and the rate of evolutionary change is likely to be underestimated. In contrast, ML uses branch lengths to model the likelihood of change along each branch. An ML analysis of the tree in Figs 1 and 2 (pectinate ultrametric tree with internal nodes of equal length), using a continuous time Markov model of trait evolution implemented by the program DISCRETE (Pagel, 1994, 1999a, <http://www.ams.reading.ac.uk/zoology/pagel/>), also favours area Y as the more likely ancestral area at internal nodes of the tree (likelihood at $t_3 = 0.70$, $t_5 = 0.69$).

Bayesian inference

Bayesian inference has the advantage over both parsimony and ML methods of trait reconstruction of taking phylogenetic uncertainty, such as topology, parameter values, and branch length estimations, into account (Huelsenbeck & Bollback, 2001; Huelsenbeck *et al.*, 2003; Pagel *et al.*, 2004; Ronquist, 2004). However, it has the same problem as other methods of not handling asymmetry.

ALTERNATIVE EXPLANATIONS

We argue that methods currently used for biogeographical reconstructions are unsatisfactory because they do not consider all nodes, typically treat process explanations as independent of each other, and/or fail to take account of likely repeated patterns such as those induced by directionality. Directional bias can mislead all tree-based reconstructions of trait evolution (Mooers & Schluter, 1999; Omland, 1999; Pagel,

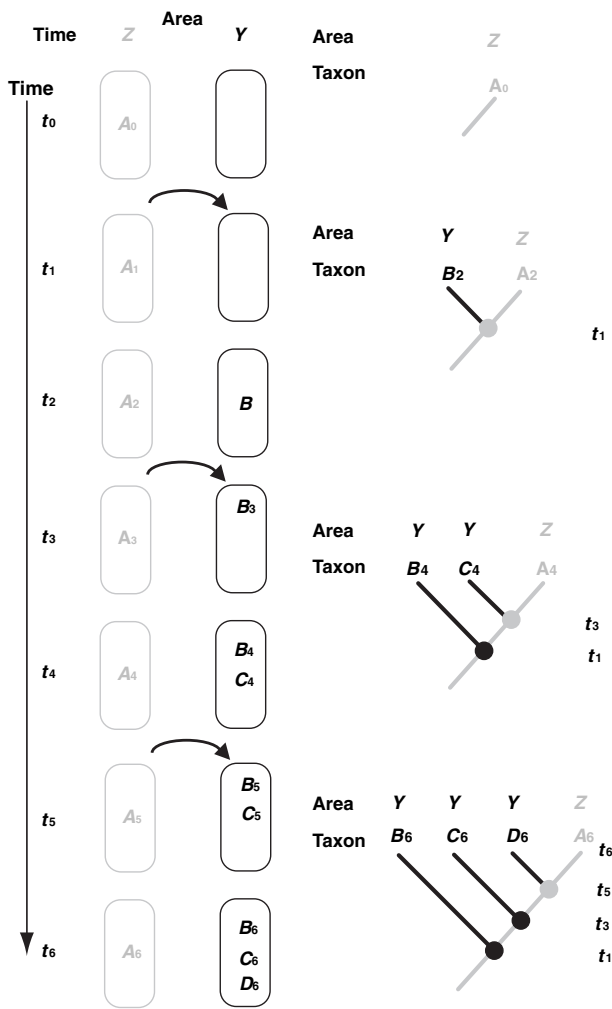


Figure 2 Stepwise sequence of dispersal events leading to the phylogeny in Fig. 1b. Boxes indicate areas and species occurring within them. Arrows show dispersal events. In the right-hand column, the area cladogram is shown as it develops through time. Shading and symbols for areas and species are as in Fig. 1. Changes in subscripts of species indicate anagenetic change. Timing of events is indicated by t_0 – t_6 .

1999b; Ree & Donoghue, 1999; Oakley & Cunningham, 2000), including ancestral areas.

Counting all nodes

Biogeographical problems are concerned with process, typically involving discrimination between vicariance and dispersal, and are hence event-based (Ronquist & Nylin, 1990). Optimizing dispersal or vicariance requires consideration of sympatric speciation (duplication), because co-occurrence of related taxa requires either speciation *in situ* or speciation in allopatry with subsequent range expansion (dispersal) to reconnect the two taxa (Ronquist, 1998). If speciation occurred in allopatry, vicariance or dispersal explanations are required, rather than implying sympatric speciation. For example, the paraphyletic residuals in area Y (Fig. 1) could each have arisen

through sympatric speciation or arisen in allopatry and then dispersed into the common area. An interpretation of sympatric speciation from the literature requires caution, however, because taxa grouped under one area by some authors may occupy discrete non-overlapping areas within that larger area and hence not be sympatric in the strict sense.

Because biogeography is process-based, all nodes in a topology need an explanation. In parsimony analysis, the total is minimized over all variables and may necessitate unparsimonious scores for some individual components (Farris, 1983). Therefore all events, including both sympatric and allopatric speciation, should be factored into the parsimony equation.

Therefore, simply (equation 1):

$$\begin{aligned} \text{total nodes} &= \text{sympatric speciation} + \\ &\text{allopatric speciation (via vicariance or dispersal)} - \text{extinction} \\ \text{i.e. } N_T &= S + V + D - E \end{aligned}$$

There are three nodes in Fig. 1, requiring a minimum of three explanations (events) for the apparent divergence and distribution of taxa.

Non-independence of variables

Analyses of taxon–area phylogenies are often performed to optimize one process, in isolation from others, in order to answer questions such as ‘how many dispersals are required to explain the current distribution of this lineage?’ However, dispersals are not independent of the other explanations for divergence events (nodes). Allopatric speciation (dispersal or vicariance) and sympatric speciation cannot occur for the same taxon simultaneously and are thus not independent of one another for explaining a node. That is, if dispersal is inferred to explain a node, then vicariance cannot simultaneously explain the same node. Similarly, if dispersal is not inferred to explain a node, another explanation (such as sympatric speciation or vicariance) is required. As pointed out above, choosing an option that minimizes the number of inferred dispersals minimizes one of the possible process explanations for nodes but it may not minimize overall parsimony for a topology because dispersal, in some cases, will explain only some nodes and other processes will need to be invoked to explain the others.

Repeated directional patterns and processes

The simplistic assumption of assigning equal probability to different kinds of evolutionary events (e.g. gains and losses) may often be unfounded (Omland, 1997; Schluter *et al.*, 1997; Cunningham *et al.*, 1998; Pagel, 1999b; Nielsen, 2002; Ronquist, 2003; Felsenstein, 2004). For example, multiple losses of features under parallel selection appears to be a common phenomenon in evolution, with some well-documented examples. Repeated loss or reduction of legs and antennae is associated with a galling habit in scale insects (Cook & Gullan, 2004). Flight appears to have been lost many

times in different lineages of pterygote insects (Whiting *et al.*, 2003), especially in historically stable, isolated (island-like) habitats (Wagner & Liebherr, 1992). Flightless species of birds also appear to have evolved repeatedly and independently following dispersal of their volant ancestors to oceanic islands (Trewick, 1997; Slikas *et al.*, 2002). Intuitively and empirically, loss of flight appears to be much more common, and easier in an evolutionary sense, than evolution of flight.

Treating each process (or trait change, or losses and gains) as being equally likely, when they are not, can have a significant effect on trait reconstruction using current methods, such as parsimony and ML (e.g. Omland, 1997, 1999; Pagel, 1999b; Schultz & Churchill, 1999; Oakley & Cunningham, 2000; Huelsenbeck *et al.*, 2002; Nielsen, 2002; Ronquist, 2003). In biogeography, the equivalent to equal rates of losses and gains is the treatment of a dispersal from *Y* to *Z* as being equally likely as a dispersal from *Z* to *Y* (Fig. 1a). The assumption does not consider the inferred process of dispersal. Whilst dispersal may be rare over time, it may be non-random in space – as shown by the examples cited above. If there is directionality to dispersal, it would be expected that there would be a high frequency for a single dispersal per taxon in that direction, a lower frequency of two dispersals per taxon in that direction, and lower still for three. However, depending on the strength of the directionality, the frequency of multiple dispersals may be higher than for a single dispersal in the opposite direction: the greater the strength of directionality, the higher the frequency of multiple dispersals in one direction relative to dispersal in the opposite direction (Fig. 5).

The source taxon of dispersing organisms may remain a single interbreeding population persisting over a long period, i.e. a cohesive gene pool changing through time, while spawning successive new populations into another area (a sink). If dispersal is non-random, this may result in a 'nested ancestral area' (NAA) – a taxon from the ancestral area appears nested within a paraphyletic group of taxa occurring in the sink area. That is, the ancestral area will appear at a terminal node in a taxon–area cladogram and is typically interpreted as 'recently colonized'.

HOW TO BECOME A NESTED ANCESTRAL AREA: AN ALTERNATIVE EXPLANATION FOR FIG. 1

As explained above, the commonly used Fitch optimization interprets the position of species *A* in Fig. 1 as a recent dispersal from area *Y* to *Z*. A converse interpretation is possible if repetitive events occur. For simplicity, extinction is assumed to be absent in the following reconstruction of such events (Fig. 2).

At time 0 (t_0), species *A* occurs in area *Z*. Species *A* usually disperses locally but there may be occasional LDDC to area *Y* (t_1). Establishment of sp. *A* in *Y* depends on the process of getting to *Y* (e.g. wind, storms), and population establishment once in *Y* (e.g. habitat it arrives in, numbers and sex of individuals). Either dispersal from area *Z* to area *Y* may be unusual (e.g. exceptional storm events) or establishment events may be rare. If events are

frequent, the disjunct populations will function as a single gene pool. However, if the period of time between dispersal/establishment events ($t_2 - t_1$) is sufficient, a subpopulation established in area *Y* may diverge from sp. *A* to become a different species (sp. *B*). We now have a sister relationship of sp. *A* in area *Z* and sp. *B* in area *Y*. Both populations will undergo anagenetic change, which is shown by their changing subscripts through time in Fig. 2 (e.g. from A_1 to A_2 over this period).

A later dispersal event (t_3) in the same direction as the first may lead to a colonization of area *Y* by sp. A_3 . Because sp. A_3 is distinct from its sister sp. B_3 , two species now occur in *Y* (A_3 and B_3). Again, there may be differentiation between the populations of sp. A_3 in areas *Z* and *Y* leading to isolation of the colonizing population in area *Y*, which becomes species C_4 (t_4). Periodic episodes of colonization of area *Y* from area *Z* (with differentiation of populations between events) could lead to multiple species in area *Y*, whilst leaving a single species in area *Z* (A_6 at t_6). Thus, on a species phylogeny, the area occupied by the original species (*Z*) would be nested within a paraphyletic area *Y*. Species *A* in *Z* will be attached to a terminal node if it undergoes anagenetic change, as expected, with character fixation between episodes of dispersal to and speciation in area *Y*. Hence it will share apomorphies with the successively dispersed new species and will appear terminal in a phylogeny. Change in a population is inevitable over time, but if dispersal events are frequent relative to allopatric speciation events, then the organismal phylogeny will be a polytomy, rather than resolved with a 'nested ancestral area'.

The NAA alternative explanation is as parsimonious as the usual interpretation if the parsimony sum is considered (equation 1 above). That is ($S + V + D - E = N_T$):

Usual interpretation: $2 + 0 + 1 - 0 = 3$ (dispersal interpretation), or $2 + 1 + 0 - 0 = 3$ (vicariance interpretation).

NAA interpretation: $0 + 0 + 3 - 0 = 3$ (all dispersal), or $0 + 1 + 2 - 0 = 3$ (if one vicariance event e.g. Fig. 3).

If dispersal from *Z* to *Y* is much more likely than dispersal from *Y* to *Z*, then the NAA explanation will also be the most likely explanation.

IMPLICATIONS OF A NESTED ANCESTRAL AREA

Failure to take account of directionality and other biases in reconstruction methods has implications beyond the simple misinterpretation of the biogeography of a taxonomic group. Several are outlined below.

Calibration of molecular dates, and their interpretation

There is no known fossil record for most taxa and it is very incomplete for others. In addition, much of the plant fossil record consists of pollen and spores that are seldom identifiable to species level and often provide little resolution within species-diverse groups, e.g. eucalypts (Hill, 1994). The relationship between pollen taxa and species-level diversity is unclear, even in well-studied taxa that have a good record of

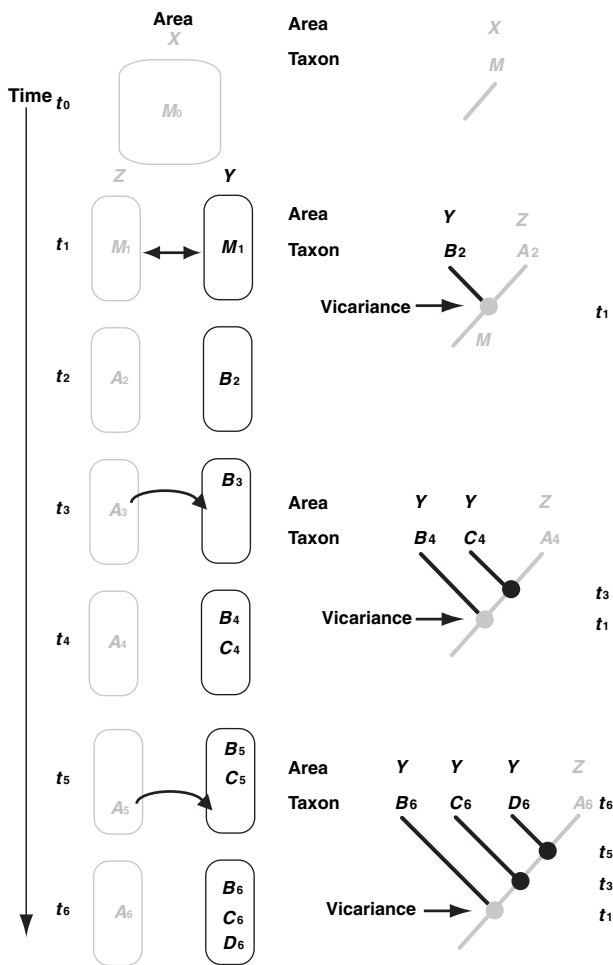


Figure 3 Stepwise sequence of vicariance followed by dispersal events leading to the phylogeny in Fig. 1b. Boxes indicate areas and species occurring within them. Arrows show dispersal events. In the right-hand column, the area cladogram is shown as it develops through time. Shading and symbols for areas and species are as in Fig. 1. Changes in subscripts of species indicate anagenetic change. At time t_0 , species M occurs in area X which vicariates at t_1 to form areas Z and Y . Taxon M speciates in allopatry to form two daughter species: A and B . Two dispersal events from area Z to area Y follow, with sufficient time between each for the populations to have speciated. The single taxon in area Z undergoes anagenetic change through time. Although a population has been present in area Z for the same length of time as it has been in area Y , conventional reading of the tree is such that area Z appears only recently colonized.

both pollen and macrofossils, e.g. *Nothofagus* (Hill, 2001). This uncertainty in the placement of fossils means that a failure to recognize a NAA situation has severe consequences for the calibration of molecular clocks. For example, if a dated fossil of the lineage is known from area Z and is used as a calibration point for molecular dating, uncertainty in its placement could cause large differences in estimates for other nodes. A fossil found in Z that is assignable to the group, but not to an individual species within the group,

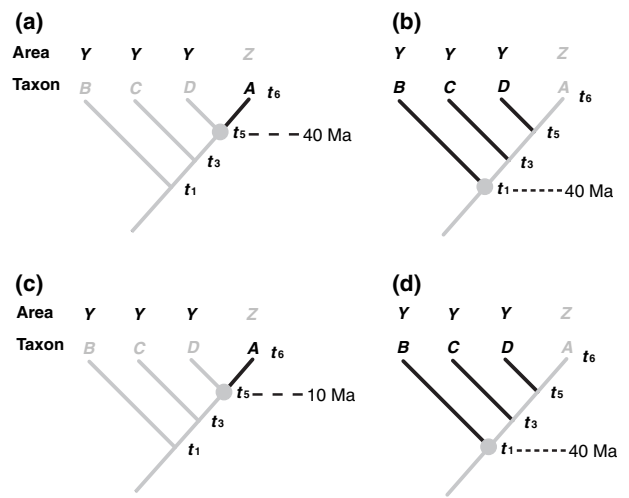


Figure 4 Implications of molecular dating of nodes under different interpretations of the taxon-area phylogeny. (a)–(b) assuming that the Z - Y split is used to calibrate the clock, e.g. a vicariance event at 40 Ma. (a) In the standard interpretation, this is also the date of the split between species A and D hence node t_5 dates at 40 Ma and node t_1 much earlier. (b) In the nested ancestor interpretation, the vicariance event may have occurred much earlier, implying a younger age for all the speciation events, e.g. $t_1 = 40$ Ma. (c)–(d) assuming independent calibration of the molecular clock, i.e. a node outside the ingroup. (c) In the standard interpretation, the split between areas Y and Z is assumed to coincide with the split between species A and D , i.e. 10 Ma. No fossils of the entire lineage are expected in Z before this date. (d) In the nested ancestor interpretation, speciation event A - D represents only the latest such split between Y and Z , with the earliest having occurred much earlier (e.g. at 40 Ma). Fossils of the lineage are predicted in Z from 40 Ma.

would typically be assigned to the terminal node. This results from a belief that the fossil could not be older because the group was not in Z until the most recent divergence event. If the fossil is placed at the most recent node (t_5) (e.g. Fig. 4c), then deeper nodes in the tree will be estimated to have older divergence times than if it is placed in the position inferred from a NAA interpretation at t_1 (Fig. 4d).

A NAA situation also has implications for discriminating between a vicariance and all-dispersal interpretation. For example, a common question in biogeography is whether a vicariance event between Y and Z may explain part of the distribution of a lineage. Hence, the timing of nodes is increasingly being used to discriminate between vicariance and dispersal (e.g. Swenson & Bremer, 1997; Renner *et al.*, 2000, 2001; Winkworth *et al.*, 2002a; Givnish & Renner, 2004). If, under a conventional reading of Fig. 1, a molecular date suggests that the most terminal node is too recent to be explained by vicariance then a dispersal explanation is typically inferred (e.g. Leys *et al.*, 2000; Trewick, 2000). However, under alternative biogeographical reconstructions for Fig. 1, another node may be the result of a vicariance event (e.g. Fig. 3). Thus, if the basal node in Fig. 1 had an estimated timing consistent with a

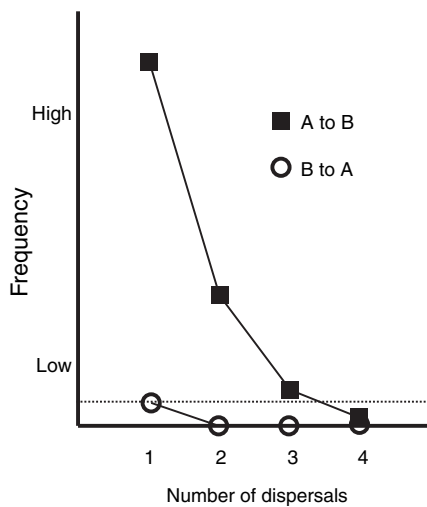


Figure 5 Directional dispersal. The frequency of multiple dispersals is likely to be lower than that for a single dispersal. Asymmetry of dispersal arises when dispersal in one direction (e.g. from A to B) is more frequent than dispersal in the other direction (B to A). In this example, it would be more likely to observe three dispersals from A to B than to see one dispersal from B to A (dotted line).

vicariance event, then vicariance should still be considered possible for explaining that part of the biogeography of the lineage. The parsimony cost for Fig. 1 would still be three if there was an early vicariance event between areas Y and Z, followed by two dispersals from Z to Y.

Conservation priorities

It has been argued that centres of origin, such as source populations, should be given higher conservation priority because such areas have spawned species in the past and may therefore be likely to do so in the future (e.g. Fjeldsa, 1994; Linder, 1995; Soltis & Gitzendanner, 1999). Under conventional ancestral area reconstruction, area Y in Fig. 1 is reconstructed as the ancestral area, whereas under a NAA scenario area Z is the ancestral area. Clearly this has implications for conservation management. The two opposing extreme hypotheses suggest different assumptions about the population histories of the taxa in those areas. Under a conventional reading, area Y might have had an unstable history in leading to speciation among local populations. In contrast, a NAA hypothesis suggests that area Z has had a long period of stability, with taxon A persisting through to the current time.

TESTING HYPOTHESES – POSSIBLE SOLUTIONS

Geological and fossil record

A good geological record can enable choice between competing dispersal hypotheses (e.g. Fig. 4a,b). For example, the

geological record may indicate that one of two terminal sister areas is continental land and much older than its sister area, a recent volcanic island. Dating of nodes, in this case, may rule out possibilities (Hunn & Upchurch, 2001; Donoghue & Moore, 2003; Page, 2003). If the common node of sister taxa, one on the island and one on the mainland, is about the same age as the island, then it seems most likely that dispersal occurred from the continent to the island, and not vice versa.

Under the conventional late dispersal (Fitch, ML) interpretation of Fig. 1, it is assumed that the lineage including species A–D was absent in area Z until the final speciation and dispersal event. Presence of fossils of that lineage in area Z older than the date of the most recent node (grey node, Fig. 1) would falsify the late dispersal hypothesis. By contrast, the NAA hypothesis assumes a continuous presence of the lineage in area Z from t_0 to t_6 . Fossils in Z from any time before t_5 would support this hypothesis, and a continuous record from t_0 to t_6 would strongly support it. Therefore, a fossil record that is older than predicted, and in conflict with conventionally read molecule-based trees, should lead to a reassessment of tree interpretation. The NAA model could explain the discrepancy between molecular and fossil estimates of the time of divergence because it predicts a longer history of the lineage in the NAA area than that determined from the most recent node on the tree. In the case of such a re-interpretation, the molecular clock estimates would need a calibration point outside the lineage in question.

Independent estimates of asymmetry

Asymmetry (directionality) can be built into character-state reconstruction methods to try to provide more realistic reconstructions of ancestral states. Approaches for doing this include step matrices (parsimony) (e.g. Ree & Donoghue, 1998; Belshaw & Quicke, 2002), rate matrices (ML) (e.g. Mooers & Schluter, 1999; Pagel, 1999a; Oakley & Cunningham, 2002; Nepokroeff *et al.*, 2003), or Bayesian prior probabilities (e.g. Schultz & Churchill, 1999). A way of using these methods is to ask the question ‘How biased does asymmetry need to be to give an alternative reconstruction of ancestral states?’ (e.g. Ree & Donoghue, 1998) and then to make a decision about whether the bias required is evolutionarily realistic. This approach has been used for morphology (e.g. loss or gain of wings in stick insects, Whiting *et al.*, 2003) and behaviour (e.g. life history strategy in ichneumonoids, Belshaw & Quicke, 2002).

For Fig. 1, the reversal in ancestral area reconstruction, from one dispersal from area Y to area Z to three dispersals from area Z to area Y, occurs when the asymmetry is coded to be $> 3 : 1$ (Fitch reconstruction, DELTRAN and ACCTRAN, as implemented in PAUP* ver. 4.0b10, Swofford, 2002). If all processes are considered, and all nodes counted (equation 1), the reversal in reconstruction can occur whenever dispersal in one direction is down-weighted relative to dispersal in other directions and sympatric speciation (i.e. parsimony sum is least for three dispersals).

The problem is that in most circumstances there is no objective way to decide whether the required asymmetry is realistic. It has been suggested that asymmetry could be estimated using comparisons across other taxa (Omland, 1999 and citations therein). However, as acknowledged by Omland (1999), estimates derived from phylogenies have the problem of circularity in that they use tree-reading to determine character transitions and therefore can be biased as a result of the same asymmetry that is being estimated (Cunningham, 1999; Mooers & Schluter, 1999; Omland, 1999). That is, the estimates are not independent of tree-reading problems and are therefore subject to the same problem of underestimation of asymmetry. To avoid the circularity of phylogeny-based asymmetry estimates, parameter values need to be derived independently of tree-interpretation, such as from biology or other known processes that can be estimated. This has not yet been attempted in biogeography.

Possible sources of independent estimates of asymmetry

Sanmartín & Ronquist (2004) estimate that 6.59% of dispersals among Southern Hemisphere taxa were from Australia to New Zealand, whereas only 3.82% were from New Zealand to Australia. That is, dispersal with the WWD was almost twice as common as dispersals against it. These values are likely to be underestimates of the real asymmetry because Sanmartín & Ronquist's estimates are based on reconstruction of character state changes (direction of dispersal) on phylogeny alone and are probably biased as a result of the asymmetry itself. Interestingly, Sanmartín & Ronquist (2004) determined that the observed number of dispersals was significantly less frequent than that expected, whereas inferred duplications (sympatric speciation) were more frequent than expected. This is the outcome that would be expected if there were multiple directional LDDCs but with trees read in the conventional manner, inferring single dispersals (forcing dispersals towards the terminal nodes of trees) and thereby requiring greater numbers of duplications to explain internal nodes. We suggest that the significant bias found by Sanmartín & Ronquist (2004) is consistent with the failure to recognize NAA situations.

However, because Sanmartín & Ronquist's (2004) estimates are likely to be underestimates, a ratio of *c.* 2 : 1 could be used as a conservative starting point to assess the possibility of multiple dispersals. That is, reconstruction of dispersal between Australia and New Zealand that can be reversed with a weighting scheme of 2 : 1 should favour a 'multiple dispersal out of Australia' hypothesis rather than an 'single dispersal out of New Zealand' hypothesis. This minimum ratio method could be extended to other areas where asymmetry is expected.

Genetic diversity

Population genetics can give an indication of direction of dispersal and could be used to derive an independent estimate of asymmetry. Populations that have been established following dispersal from a parental population are expected to

exhibit only a proportion of the genetic diversity of the parental population (Templeton, 1998). This is because they have been sampled from the parental population (via dispersal) – only some individuals from the parental population contribute to the daughter population. Thus, the relationship between two populations in different areas could be considered when deciding which represented the putatively dispersed population. For example, consider terminals *A* and *D* in Fig. 1 to represent two populations of the one species. If population *A* comprised genetic diversity greater than, and encompassing, that of population *D*, we could be more confident that *A* represented the ancestral population, at least for population *D*.

Dean & Ballard (2004) provide an empirical example of reconstruction of ancestral area using population genetics and phylogenetics for *Drosophila simulans*. Similar studies provide evidence for directional migration among populations, particularly for marine invertebrates, including sea-stars (Waters & Roy, 2004) and barnacles (Wares *et al.*, 2001). Multiple invasions from stable source populations into new or unstable habitats have also been inferred from population genetic studies. Three-spined sticklebacks are thought to have repeatedly colonized and speciated into fresh-water lakes from a marine source (*Gasterosteus aculeatus*) in the Strait of Georgia, British Columbia, when sea levels rose twice during the Pleistocene (Taylor *et al.*, 1997; Taylor & McPhail, 2000; Schluter *et al.*, 2001).

The phylogeographical pattern that would be expected during the early stages of directional dispersal leading to a NAA situation has been recorded for *Galaxias maculatus* (Waters *et al.*, 2000b). This fish occurs in coastal waters of Australia (Tasmania), New Zealand and Chile. The three regions form discrete haplotype clusters, with the exception of a haplotype from one individual from New Zealand that clearly clusters with the Tasmanian group. The divergence between the Tasmanian and New Zealand clusters suggest that gene flow is not common, but that a rare dispersal event (only one individual sampled) may have occurred from Tasmania to New Zealand in the direction of the west to east ocean currents (Waters *et al.*, 2000b).

Unfortunately, a genetic diversity argument cannot be applied unambiguously to taxa that are no longer part of the one gene pool (i.e. different species). Gene pools diverge through time and different population sizes, gene coalescence times and selection pressures will affect genetic diversity. For example, the original source population could undergo a severe bottleneck and lose diversity such that it now appears less diverse than its daughter. That is, over time, the differing evolutionary pathways of separate species will obfuscate population histories.

To avoid these problems, an alternative use of population genetics and phylogeography could be to examine extant species that are shared across areas of interest. An estimate of direction of dispersal could be determined across populations of multiple taxa and used to derive an estimate of asymmetry unbiased by tree-reading. For example, if 90 of 100 species

shared between two areas, such as *Y* and *Z*, were determined to have originated in *Z*, then an asymmetric weighting scheme of 9 : 1 could be built into ancestral area reconstruction for a higher level group occurring in these two areas. This method assumes that conditions leading to the observed asymmetry were also present at the time of divergence of taxa in the focal group. Testing this assumption requires additional information, for example, from climatic reconstructions for the period in question. Additionally, the biology of different organisms varies and therefore the causes and magnitude of asymmetry will vary among taxa. Account could be taken of this in estimating asymmetry between regions and using species with similar life-history traits to the taxon of interest.

Australia and New Zealand currently share many species (e.g. Jordan, 2001; McGlone *et al.*, 2001; Mummenhoff *et al.*, 2004), providing a rich resource for estimating asymmetry in dispersal between the two regions if population level studies were to be conducted.

AN EXAMPLE OF A POTENTIAL NESTED ANCESTRAL AREA SCENARIO

Australia and New Zealand provide a situation conducive to the development of NAA patterns. Although the two land masses first separated 85 Ma (Kroenke, 1996; Lee *et al.*, 2001), when New Zealand rifted from Antarctica, they are currently separated by only 2000 km of ocean – a distance that has been relatively stable for 55–60 Ma (Pole, 1994; Kroenke, 1996). Additionally, the two regions extend into the southern latitudes of the Southern Hemisphere dominated by the ACC and WWD. It would therefore be predicted that dispersal should most often occur in the direction of the WWD from Australia to New Zealand, and this has been postulated as the cause of the high number of shared species between the two countries (e.g. Raven, 1973; Jordan, 2001; McGlone *et al.*, 2001).

However, it has also been suggested that dispersal has occurred against the prevailing winds and ocean currents – from New Zealand to Australia (e.g. Wardle, 1978; Swenson & Bremer, 1997; Wagstaff *et al.*, 2002; Winkworth *et al.*, 2002a; Sanmartín & Ronquist, 2004). The recent reconstructions have been based on the finding of Australian taxa nested within New Zealand groups and, implicitly, an assumption of equal probability of dispersal in all directions, i.e. random dispersal. In the above cases, it is acknowledged that this is against the direction expected and authors have invoked unknown alternative processes to explain the apparent anomaly.

We reanalysed the three data sets that contain taxa with distributions including both Australia and New Zealand that were used by Winkworth *et al.* (2002a) to support their ‘out of New Zealand’ hypothesis. Interestingly, although the expected direction of dispersal is, as acknowledged by Winkworth *et al.*, with the westerly winds from Australia to New Zealand, no dispersal in this direction is inferred in any of the three data sets. That is, despite four or five inferred dispersals from NZ to Australia (two in *Ranunculus*; one or two in *hebes*; one in

Myosotis), none are inferred to have gone in the expected eastwardly direction. We do not suggest here that dispersal could not have been against prevailing winds, and the authors give plausible scenarios for such dispersal. Rather, we use the phylogenies presented by Winkworth *et al.* (2002a) because they represent a recent study and provide a framework to demonstrate that alternative explanations could be considered.

Phylograms were captured from original publications (Lockhart *et al.*, 2001; Wagstaff *et al.*, 2002; Winkworth *et al.*, 2002b) using TreeThief v1.0 (Rambaut, 1999, <http://evolve.zoo.ox.ac.uk/software.html?id=treethief>). To determine the level of asymmetry required to reverse the ‘out of New Zealand’ findings, we used Fitch parsimony (ACCTRAN and DELTRAN), as implemented in PAUP* ver. 4.0b10 (Swofford, 2002), and ML using a continuous time Markovian model (Pagel, 1999a), as implemented in DISCRETE (Pagel, 2000) and MULTISTATE (Pagel, 2003, <http://www.ams.reading.ac.uk/zooloogy/pagel/>).

Parsimony

In all three data sets, unweighted Fitch parsimony (acctran and DELTRAN) reconstructed New Zealand as the ancestral area at all nodes containing Australian taxa, thereby inferring dispersal from NZ to Australia. We applied asymmetry, in favour of west to east (i.e. Australia to NZ), to the direction of inferred dispersal by using asymmetrical step-matrices with weight ratios ranging from 2 : 1 to 7 : 1. A change in inferred direction of dispersal, from a New Zealand ancestor to a reconstruction of an equivocal or Australian ancestor, occurred with a ratio of 2 : 1 for *hebes*, 4 : 1 for *Ranunculus*, and 6 : 1 for *Myosotis* (Table 1). In other words, if dispersal from Australia to New Zealand is more than six times more

Table 1 Fitch-parsimony estimates of ancestral areas in examples used by Winkworth *et al.* (2002a). Asymmetrical rate matrices (indicated) were applied to dispersal direction, favouring Australia to New Zealand

	<i>Hebes</i>	<i>Ranunculus</i>	<i>Myosotis</i>
Basal node; 1 : 1	NZ	NZ	NZ
Basal node; 2 : 1	Aus or NH	NZ	NZ
Basal node; 3 : 1	Aus	NZ	NZ
Basal node; 4 : 1	Aus	Aus or NZ	NZ
Basal node; 5 : 1	Aus	Aus	NZ
Basal node; 6 : 1	Aus	Aus	Aus (a), NH (d)
Basal node; 7 : 1	Aus	Aus	Aus
Other Aus-NZ nodes; 1 : 1	NZ	NZ	–
Other Aus-NZ nodes; 2 : 1	NZ	NZ	–
Other Aus-NZ nodes; 3 : 1	Aus	NZ	–
Other Aus-NZ nodes; 4 : 1	Aus	Aus or NZ	–
Other Aus-NZ nodes; 5 : 1	Aus	Aus	–
Other Aus-NZ nodes; 6 : 1	Aus	Aus	–

Results were the same for ACCTRAN (a) and DELTRAN (d) reconstructions, except where indicated.

Aus, Australia; NZ, New Zealand; NH, Northern Hemisphere.

Table 2 Maximum likelihood estimates of ancestral areas following re-analysis of data from Winkworth *et al.* (2002a) using a Markov continuous time model implemented in DISCRETE

Rate bias towards NZ	<i>Hebe</i>				<i>Ranunculus</i>				<i>Myosotis</i>			
	Rate low		Rate high		Rate low		Rate high		Rate low		Rate high	
	Basal node	Other nodes	Basal node	Other nodes	Basal node	Other nodes	Basal node	Other nodes	Basal node	Other nodes	Basal node	Other nodes
5 to 1	50	71–79	50	83	100	98–100	50	83–87	100	100	66	83
2 to 1	51	65–76	50	67	100	99–100	54	66–83	100	100	80	71
1 to 1	65	81–92	50	50	100	100	66	51–83	100	100	89	70
1 to 2	65	69–78	50	33	100	100	59	34–67	100	100	88	44
1 to 5	51	25–31	50	17	100	100	51	17–33	100	100	85	17

Values are preference for New Zealand (> 50) or Australia (< 50), expressed as a percentage. Preference for Australia is shown in bold.

common than in the other direction, reconstructions for all three of these taxa favour Australian ancestors for the New Zealand clades. Notably, the change for hebes occurred with a directional bias of only 2 : 1.

Likelihood

MULTISTATE was used to model multiple areas in addition to Australia and New Zealand, such as New Guinea and South America. Although all three MULTISTATE data sets failed to meet the optimal ratio of terminal taxa to parameters (Pagel, 2003), the results from MULTISTATE analysis did not differ qualitatively from those of the DISCRETE analysis, and only the latter are presented here (Table 2). The terminal taxa from areas other than Australia and New Zealand were pruned from the data sets used in DISCRETE. For the hebe data set, we compared results using uncorrected branch lengths with those using local rate smoothing (NPRS) as implemented in TreeEdit v1.0a10 (Rambaut & Charleston, 2002, <http://evolve.zoo.ox.ac.uk/software.html?id=treededit>). The results were not qualitatively different and only those from the rate-smoothed tree are reported here.

The Markovian ML model implemented in DISCRETE was unable to reconstruct a NAA scenario from any of the three data sets. Allowing the model to estimate the rates of dispersal from the trees gave the same result for all three data sets: (1) a higher rate in the direction of Australia and (2) a strong preference for New Zealand as the ancestral area at most internal nodes (not shown). Constraining ranges of rates for both asymmetric and symmetric dispersal (Table 2) also gave a strong preference for New Zealand as the ancestral area at most internal nodes in most cases. The only constraints that led to reconstructions preferring Australia as the ancestral area were the combination of high dispersal rates with a strong bias towards Australia (shown in bold in Table 2). This is the opposite of the NAA scenario, which predicts a dispersal rate bias towards New Zealand, from an ancestral area in Australia. However, when dispersal rates were constrained with a bias towards New Zealand, NZ was always reconstructed as ancestral, in all three data sets (Table 2).

This result seems paradoxical compared with the parsimony results and the expectation of the NAA scenario. The following is how we interpret what the Markovian model is doing. When the instantaneous transition rates (dispersal rates) are high, multiple changes occur along each branch, and the estimates of ancestral states tend to reflect directly the relative rates, irrespective of the terminal states. This can be clearly seen in the high-rates results for 'other nodes' in the rate-smoothed hebe data (Table 2). When the dispersal rates are low, it is unlikely that there will be change along any branch, and the reconstructions tend to reflect the predominant state among terminal taxa. In all three data sets, New Zealand is by far the most common terminal taxon and, in all three, this area is strongly favoured in reconstructions when rates are low (Table 2). A NAA scenario requires both (1) Australia to be ancestral at the nodes along the backbone of the phylogeny, and (2) the terminal states to be predominantly New Zealand. This implies lack of change (stasis) in states along the backbone of the tree, with all the change (dispersals) occurring in the terminal branches (with a strong bias towards New Zealand). The Markovian ML model appears to be unable to model this differential pattern of evolution over the tree, and so cannot reconstruct a NAA scenario. This finding is similar to that shown by Oakley & Cunningham (2000) for continuous, rather than discrete, directionally biased traits.

Of the three taxa discussed above, two species (*Chionohebe densifolia* and *Myosotis australis*) allow the possibility of using population genetics and phylogeography to attempt to determine the direction of dispersal because they are apparently shared between Australia and New Zealand. Similarly, *Hebe elliptica* is shared between NZ and the Falkland Islands and could be used to assess direction of dispersal between these two localities.

CONCLUSIONS

This paper demonstrates that there are plausible alternative biogeographical reconstructions for taxon–area phylogenies that are currently not being considered. This is mainly because tree topology is given primacy over biogeographical processes.

Additionally, inferences about non-terminal speciation events (the cause of internal nodes in taxon phylogenies) that are implicit in many reconstructions (e.g. sympatric speciation) are ignored. Consideration of all factors (phylogeny, process, speciation and fossils) is required to enhance our interpretation of biogeography. In particular, the effects of possibly asymmetrical dispersal should be considered.

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BIOSKETCHES

Lyn Cook has interests in speciation, molecular phylogenetics, biogeography, karyology and scale insect–plant interactions.

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