Molecular studies have documented high levels of geographic structure in most plant and animal groups and this finding has fundamental implications for the science of biogeography. The fascinating depth and detail of the geographic structure, together with the repetition of patterns in unrelated groups, all threaten to undermine the main theory of twentieth century biogeography – speciation by chance dispersal. Ever since the influential study by Matthew (1915), dispersal theory has dominated the field. The idea that dispersal is a mode of speciation and not just the movement of organisms is still often accepted as a fact, even in molecular work. Biologists producing molecular phylogenies sometimes suggest that their work has ‘revealed’ chance dispersal, but in a scientific study it is the facts that everyone agrees on – not inferences and interpretations – that are revealed. The molecular studies have indeed revealed spectacular distribution patterns that can be accepted as ‘facts’, at least for the purposes of discussion, but the underlying causes of these facts are much less obvious.

The distribution patterns shown in the new molecular work are interpreted here with reference not to chance, but to a small number of geological and climatic revolutions. These include pre-breakup tectonics in Gondwana (extension and magmatism), the rifting of Gondwana, and the last, great marine flooding in the mid-Cretaceous, probably caused by a combination of tectonic and climatic events. This approach does not deny that chance dispersal exists, but the focus here is on repeated patterns, not on idiosyncratic distributions found in only one or a few groups.

In the Modern Synthesis, chance dispersal is the main mode of speciation. Following its origin by dispersal across a barrier, a group then attains its distribution by a second dispersal, a range expansion outwards. In contrast, during a vicariance event different clades develop from a common ancestor that was already widespread, and each new clade originates at the same time as its distribution, more or less in situ. The debate concerning the relative importance of dispersal and vicariance had begun by the end of the Enlightenment, around the same time that evolutionary theory was introduced (White, 1789 [1977: 65]; Willdenow, 1798: 430 [as quoted in Weimarck, 1934]). Since then, ideas on evolution have changed in many ways, but the vicariance versus dispersal debate has continued, unresolved, to the present day.

Most writers over the millennia have assumed that distribution patterns are caused by physical movement – ‘dispersal’. All organisms move, and, with a few exceptions, every individual organism has moved to its current location. In addition, while the distribution of a clade is represented on a map with dots or lines, it is in fact mobile,
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Fig. 1.1 The distribution of a hypothetical group, A. Its centre of origin might occur in the area with a highest diversity in the group (1), in the region of the oldest fossil (2), in the area of the most ‘advanced’ form (3), in the area of the most ‘primitive’ form (4), or in the area of the basal group (5). (From Michael Heads, Molecular Panbiogeography of the Tropics. ©2012 by the Regents of the University of California. Republished by permission of the University of California Press.)

or at least at a dynamic equilibrium. Likewise, if evolution involved only vicariance, every small area on the Earth’s surface would have only one type of organism and it would be endemic there. This is far from the case and so, again, there must have been movement. Yet although physical movement is universal in all (or almost all) individuals and has occurred in many clades, it does not account for all aspects of distribution. Many phylogenetic/geographic breaks have instead resulted from cessation of movement or at least a decrease in the rate of interchange among populations.

The question is not so much whether dispersal or vicariance has occurred, but whether dispersal and speciation are the result of chance movement of individual organisms or general, underlying causes such as geological change. ‘Dispersal biogeography’ is a research programme that explains the geographical distribution of organisms based on processes of dispersal, while ‘vicariance biogeography’ explains distribution with reference to geological events (Gillespie et al., 2012). In vicariance theory, range expansion and speciation (vicariance) are both caused by geological change (for example, marine incursion or mountain building). In dispersal theory, neither is – range expansion and speciation with long-distance dispersal occur in different groups at different times and are both due to chance.

Models of spatial evolution in biogeography

The centre of origin model

If a hypothetical group of plants or animals, A, has a geographical distribution as shown in Figure 1.1, how did the distribution develop? Most authors have accepted that the group originated in a restricted area and migrated outwards from there. Researchers locate this ‘centre of origin’ or ‘ancestral area’ using different criteria (Fig. 1.1). For a particular group, different methods locate the centre of origin in the area of: maximum
diversity of forms, the oldest fossil, the most ‘advanced’ form (Darwin, 1859; Briggs, 2005), the most ‘primitive’ form (Mayr, 1942; Hennig, 1966), or, in most modern studies, the ‘basal’ member of the group.

Bremer (1992) justified the search for a restricted centre of origin, reasoning that most modern species of Asteraceae, for example, are endemic to a single continent, and so the ancestor of the group would have been the same. Yet this denies the possibility of evolution in aspects of the group and there is no need to assume that ancestral taxa had the same ecology, range size, variability, or evolvability as their modern descendants. A centre of origin approach has been continued by modern authors, and programmes designed to find the centre of origin are popular. These include DIVA (‘dispersal–vicariance’; Ronquist, 1997) and DEC (dispersal–extinction–cladogenesis analysis) implemented in LAGRANGE (Ree and Smith, 2008). In certain cases DIVA will indicate widespread ancestors, contradicting the core assumption of the centre of origin approach and instead supporting vicariance. DEC, in contrast, is guaranteed to locate a centre of origin (Clark et al., 2008).

The vicariance model: differentiation of a widespread ancestor

In an alternative to the centre of origin model, the group A can be considered not on its own, but together with its closest relative, or sister-group, B (Fig. 1.2). In this pattern, analysed samples from different localities in the respective areas of A and B show a phylogeny: (Aⁱ, A², A³ . . .) (B¹, B², B³ . . .). In other words, groups A and B show reciprocal monophyly; they are sister-groups and neither is related to any particular population of the other. In Figure 1.2 the distributions of the two sister-groups show precise allopatry. The pattern is compatible with each of the two groups having arisen not by spreading out from a point, but by geographic (allopatric) differentiation in situ. In this model, each group has evolved in its respective area, from a widespread ancestor that occurred throughout the areas of both A and B. This process, vicariance, is dominated by differentiation between the two populations; any physical movement of individuals between them is of less importance. In vicariance analysis, the aim is to find the originary break between the groups, not a point centre of origin within a group. The focus is not
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Fig. 1.3 Four groups A–D with allopatric distributions in areas A–D. The phylogeny of the four groups is also shown. (From Michael Heads, Molecular Panbiogeography of the Tropics. ©2012 by the Regents of the University of California. Republished by permission of the University of California Press.)

on the group itself or on details of its internal geographic and phylogenetic structure, but on its geographic and ecological relationship with its sister. In a vicariance model, many younger groups have a distribution that is more or less the same as the ‘centre of origin’.

In a phylogenetic tree diagram, two sister clades are shown joined at a node. A node is also expressed on the Earth’s surface as a geographic boundary between two or more distributions. In a vicariance interpretation, a node does not represent a centre of origin or an ancestor, but a phylogenetic and biogeographic break or division, where two or more related groups have diverged from a common ancestor.

Origin of the ancestor

If the two descendant groups, A and B in Figure 1.2, originated by vicariance, what about their widespread ancestor? Was its wide range achieved by dispersal? That would be one possibility, but the ancestral group itself could have originated as an allopatric member of a widespread complex (Fig. 1.3). In this case, again, the group did not attain its distribution by spreading out from a localized centre of origin. The same pattern of allopatry can extend to additional relatives in other areas, and widespread or even global series of allopatric forms occur in many plants and animals. In contrast, in the centre of origin theory, each of the four allopatric groups in Figure 1.3 has a separate centre of origin within the group’s area and the distributions have no direct relationship with the groups’ origins – the groups form first and their distributions develop later. In this approach, the mutual boundaries of the four groups in the figure are secondary; the ranges only meet after the four individual groups each spread out from their respective centres of origin. Instead, in vicariance theory, the mutual boundaries are attributed to phylogeny. These breaks or nodes tend to recur at the same localities in many different
Fig. 1.4 Four groups A–D with allopatric distributions in areas A–D. The phylogeny of the four groups is also shown. Numbers and black arrows indicate traditional centres of origin and dispersal routes. White arrow at zone of overlap indicates local range expansion in clade C. (From Michael Heads, *Molecular Panbiogeography of the Tropics*. ©2012 by the Regents of the University of California. Republished by permission of the University of California Press.)

groups, often with different ecology and means of dispersal, and so a chance explanation is unlikely.

If the groups in Figure 1.3 have a phylogeny: D (C (B + A)), as indicated in the figure, this represents a simple geographic sequence of differentiation in a widespread ancestor that has proceeded from east to west: D versus the rest, then C versus A + B, then A versus B. Often there is no simple geographic progression in the differentiation sequence, and this is shown in Figure 1.4. The groups have a phylogeny: A (B (C + D)) and so the sequence of differentiation ‘jumps’ from the first node (between A and the rest) to the second (between B and C + D) and then back to the middle (between C and D). The allopatry has developed by normal vicariance in a widespread ancestor. Localized centres of origin for each of the four clades (1–4 in Figure 1.4) and dispersal from these (black arrows) are not necessary.

**Subsequent range expansion leading to geographic overlap**

The overlap between groups C and A in Figure 1.4 (white arrow) is the result of range expansion of C after its origin. This has developed as a secondary process following the origin of the four groups by vicariance and allopatry. Simple range expansion occurs by the group’s normal, observed means of dispersal and does not involve any phylogenetic differentiation. More extensive overlap is discussed further below.

**Allopatric groups that show reciprocal monophyly**

One common distribution pattern involves a group that occurs on a continent or mainland, A, and its sister-group that occurs on a smaller, offshore island, B (Fig. 1.5). The island
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Fig. 1.5 Distribution of two sister-groups, A and B. The phylogeny is: \((A_1 + A_2 + \ldots + A_7)(B_1 + B_2)\). (From Michael Heads, *Molecular Panbiogeography of the Tropics*. © 2012 by the Regents of the University of California. Republished by permission of the University of California Press.)

group is often assumed to have been derived from the mainland group by dispersal. This hypothesis predicts that island forms will be related to particular populations in their large sister-group, representing source regions. Yet well-sampled molecular studies show that in many of these cases the phylogeny instead has the pattern: \((A_1, A_2, A_3 \ldots ) (B_1, B_2, B_3 \ldots )\), with the superscripts indicating the different sample sites within areas A and B. The two groups in the two areas show reciprocal monophyly and the group in B is not related to any one population in A. In this type of pattern, dispersal can still be proposed as an explanation, but only if it occurred just once, and prior to any other differentiation in the group, and this is often unlikely. On the other hand, reciprocal monophyly is the standard signature of simple vicariance of a widespread ancestor at a break between A and B. Even if groups in the two areas A and B do not show reciprocal monophyly, a vicariance origin is still possible and this is discussed next.

‘Basal’ groups and centres of origin

A clade often has its basal phylogenetic break between a small group, with just a few species, and its more diverse sister-group (cf. Fig. 1.5). The smaller group is termed ‘basal’, although in fact only the nodes are basal; no group is more or less basal than its sister. ‘Basal group’ is a useful term for a smaller sister-group, but there is no reason to assume that a basal group is more primitive than its sister, or is the ancestor of its sister. The basal clade in a group is often interpreted as occupying the centre of origin for the group, but, again, this assumption is not warranted. There is no reason why the basal group, rather than its sister, should represent the centre of origin, the time of origin, the ancestral ecology or the ancestral morphology of the group as a whole. The focus instead should be on the phylogenetic and geographic details of the break between the two sister-groups.
Models of spatial evolution in biogeography

Interpreting phylogenies as sequences of vicariance events, rather than sequences of dispersal events

In the Modern Synthesis, the sequence of nodes in a phylogeny is read as a sequence of dispersal events. The centre of origin is occupied by the basal group, with subsequent taxa invading a new region, differentiating and adapting, and then invading the next region. Instead, as indicated above, the sequence of nodes can represent a series of differentiation events in an ancestral complex that was already widespread.

Groups with a basal grade in one region

In many groups the subgroups show simple allopatry (Fig. 1.3) or minor overlap (Fig. 1.4). Other groups show more extensive overlap. In one common pattern, groups have a basal grade, a paraphyletic group, in one area, A, and a disjunct group in another area, B (Fig. 1.6). In centre of origin theory, the phylogeny of this pattern, for example, A (A (A (A+B (A)))), is explained as the result of dispersal within the clade, from A to B. Nevertheless, this cannot be assumed, as the ancestor may have already been widespread in both A and B (Fig. 1.6A). Allopatric differentiation around a node in A (Fig. 1.6B, C), and extinction of populations between A and B leads to a basal grade in area A (Fig. 1.6D). Subsequent local overlap can occur in area A, but even if the clades develop substantial overlap they often show slight but significant differences in their distribution (Fig. 1.6D) and these may represent traces of the original allopatry. Many biogeographic studies code all the species in areas equivalent to A in the same way, lumping them together and overlooking minor but critical differences.

The origin of the whole clade shown in Figure 1.6 is a separate question from the origin of the differentiation within it, and is not discussed here. The origin of a group cannot be deduced from the phylogeny or biogeography of the group itself; it requires comparison with the group’s relatives.

A vicariance analysis of the pattern with a basal grade in one region, shown in Figure 1.6, infers local overlap within A by normal means of dispersal. Instead, a dispersal analysis suggests long-distance dispersal from A to B, often by unusual or extraordinary means. An actual example of the hypothetical pattern shown in Figure 1.6 is the subtribe Arctotidinae in the plant family Asteraceae. The group comprises a basal grade of three southern African clades, a clade including *Cymbonotus* of southern Australia, and its sister-group, a diverse southern African clade (Fig. 1.7; Funk et al., 2007; McKenzie and Barker, 2008). Note that *Cymbonotus* is embedded in an Australian–southern African clade, and the Australian representation is not just a secondary, derivative outlier. The five main clades are all present in Africa but it is likely that there are significant differences in the distributions.

Figure 1.6 suggests that in a simple, common case of evolution, the location of a basal grade will not indicate a centre of origin; this argument also applies to ecology and the idea of ancestral habitat. For example, an ecological phylogeny for a group: (freshwater (freshwater (freshwater (saline lakes)))), will not always mean that the saline lake clade was derived from freshwater habitat. The ancestor of the whole group may have already
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Fig. 1.6 A hypothetical example of evolution in a taxon found in two areas. (A) A widespread ancestor. (B) The ancestor begins to differentiate around a node (star) associated with the formation of a mountain range or inland sea, for example. (C) The ancestor has differentiated into five allopatric clades, four with a narrow range and one widespread. Their ranges begin to overlap while some of the populations of the widespread clade suffer extinction (broken line). (D) The clades now overlap but the ranges still show traces of their original allopatry. Following extinction of populations between areas A and B, the outlier in area B may appear to be a secondary feature and the result of long-distance dispersal from area A. (Reprinted from Heads, 2009b, by permission of John Wiley & Sons.)

Fig. 1.7 The phylogeny and distribution of clades in the Arctotidinae (Funk et al., 2007; McKenzie and Barker, 2008). (Reprinted from Heads, 2009b, by permission of John Wiley & Sons.)
occupied both freshwater and saline habitat before the differentiation of the groups, and this is even more likely if the ancestor was widespread.

A critique of the popular program DIVA admitted that it ‘reconstructs histories accurately when evolution has been simple; that is, where speciation is driven mainly by vicariance’ (Kodandaramaiah, 2010). But for a simple area phylogeny: (A (A (A, B))), programs such as DIVA and DEC (in LAGRANGE) will always find a centre of origin in A and dispersal from A to B, even if the ancestor in fact occurred in both A and B, and evolution proceeded entirely by vicariance (in area A). In this case the only dispersal was local range expansion within area A (Fig. 1.6).

The DEC model (Ree and Smith, 2008) assumes that if an ancestor is widespread across two or more areas, lineage divergence can only occur between a single area and the rest of the range, or between a single area and the entire range. It does not include a mechanism for the subdivision, in a single step, of a widespread ancestral range (comprising more than three unit areas) into two allopatric daughter ranges each comprising more than one unit area. The model requires secondary dispersal and extinction events to explain this case of normal vicariance. Many DEC analyses assume that ancestral range of a group should be similar in spatial extent to those of the living species, and this rules out a simple vicariance origin for allopatric species (see Heads, 2012a, Chapter 6).

In a valuable critique, Arias et al. (2011) observed that programs such as DIVA and DEC are based on discrete, pre-defined areas and that the definition of the areas, carried out prior to analysis, is far from trivial. Arias et al. instead suggested switching the focus away from relationships among pre-defined areas, onto the actual geographic breaks among the clades. This approach is adopted here.

Groups with a basal grade in one region and widespread apical clades

Asteraceae

Asteraceae, with ~24 000 species, is the largest plant family. The five basal branches in the family are all small groups with all or most of their members restricted to South America, while one of the apical clades is widespread (Fig. 1.8; Panero and Funk, 2008). Instead of a centre of origin in South America, the pattern suggests differentiation of a worldwide ancestor mainly at breaks in what is now South America. Following the differentiation, the diverse worldwide clade has expanded its range to include most of South America, overlapping with the basal clades there.

While the family is very large, the number of global clades in the distal group is quite small (several of the larger tribes and subtribes, some large genera). This means that through the history of the family, only a small number of widespread ancestors have existed; large groups in the family, such as the tribes Senecioneae and Astereae, each require their own global ancestor. These few ancestors have each undergone a phase of mobilism and range expansion during which they each occupied much of Earth’s land surface, before settling down into a subsequent phase of immobilism and differentiation.
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A worldwide bee: *Hylaeus*

The colletid bee genus *Hylaeus* has about 600 species, with 170 in Australia. Kayaalp *et al.* (2013) sampled 74 species and found the following phylogeny (Aus = Australia):

(Aus and New Zealand (Aus (Aus (Aus (Aus (Aus (world except Aus))))))

The overall distribution conforms to the pattern shown in Figure 1.6 and can be explained by vicariance in a worldwide group, followed by overlap (dispersal) within Australia. The non-Australasian samples make up a single, allopatric clade and Kayaalp *et al.* (2013) described this as ‘particularly striking’. In a vicariance model it is a case of simple vicariance but the authors adopted a dispersal/radiation model with a centre of origin in Australia and they discussed some of the questions this raises. For example, why has there been no back-migration of the worldwide clade into Australia, despite the convergence of Laurasia and Australia through the Cenozoic? Kayaalp *et al.* (2013) cited home advantage, which seems reasonable and also applies to a vicariance model. The authors also discussed another conundrum: ‘what kinds of biogeographical and ecological factors could simultaneously drive global dispersal [in the single widespread clade], yet strongly constrain further successful migrations out of Australia when geographical barriers appear to be weak?’ Kayaalp *et al.* argued that initial dispersal into new niches and enemy-free spaces would have been possible, but that subsequent dispersal by other lineages into the same areas would have been prevented because no further niche-space was available. Nevertheless, the other clades of *Hylaeus* show extensive overlap within Australia (along with some interesting differences; *Atlas of Living Australia*, 2012), and this contradicts the argument.

Kayaalp *et al.* (2013) concluded that: ‘Biotic composition of a region may be determined more by the early appearance of dispersal opportunities than by later relaxation of geographic dispersal barriers.’ [Italics added.] This seems reasonable