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GUEST EDITORIAL

What is a node?

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ABSTRACT

Biogeographic nodes can be characterized as sites of biological endemism, high diversity, distribution boundaries, anomalous absences, disjunct populations, taxonomic incongruence, parallelism and altitudinal anomalies. Their interpretation has depended on the evolutionary model used, in particular the mode of speciation: Croizat's vicariance or Mayr's 'peripatric' or 'founder dispersal' (=Darwin's 'chance dispersal', Hennig's 'speciation by colonization'). All authors agree that the first process, together with movement of individual organisms and diaspores, occurs, but the second is much more controversial, with panbiogeographers and many geneticists denying its importance. Although nodes have often been interpreted as centres of origin – as in refugium theory – this is not accepted here as it fails to account for their constituting both centres and margins of distribution as well as zones of absence. Instead they are interpreted as sites of vicariance related to different kinds of tectonic activity which have been shown to occur in the same locality, such as terrane accretion, subduction, regional metamorphism, granitization, volcanism, faulting, folding, uplift, subsidence and regression of epicontinental seas. It is concluded that the identification of nodes is a more productive approach to biogeographic analysis than dividing a study area into 'biogeographic regions', which are usually based firmly on current geography and represent geological and biogeographic composites.

Keywords

Panbiogeography, vicariance, dispersal, evolution, speciation, ecology, centre of origin.

> 'Nature is an endless combination and repetition of a very few laws. She hums the old well-known air through innumerable variations.' (Emerson, 1985) *History*
>
> 'A scholar's strength consists in concentrating all doubt onto his special subject.' (Canetti, 1962) *Auto da Fé*

INTRODUCTION

Biological phenomena manifest themselves through reiteration, repetition, replication and reproduction. Nothing significant in biology happens only once. Whether in space (biogeography), time (evolution) or form (genetics, morphology) biological structure is built up by the same thing being repeated, once, twice, or many times.

In biogeography, certain place names come up regularly in discussion as being especially significant in many plant and animal distributions. Panbiogeographic analysis in particular results in the recognition of these 'nodes', such as globally important ones at Guatemala/S Mexico, Chocó district in Colombia, the Guyana highlands, the Fouta Djallon Plateau in Guinea, SW Cape Province and Madagascar in Southern Africa, the region around Wallace's Line in Indonesia, and New Caledonia. Additional, locally significant nodes are usually well known to the resident naturalists, for example the John Crow Mountains in Jamaica, the Atewa Range in Ghana, the Chimanimani Mountains in Zimbabwe, Aceh in Indonesia, the Upper Watut Valley in New Guinea, NW Nelson and Fiordland in New Zealand and Taveuni in the Fiji Islands.

WHAT IS A NODE?

Diamond & Hamilton (1980) considered it very significant that for African birds, centres of species richness are also centres of endemism and foci of populations of disjunct species. Crisp *et al.* (2001) found a similar phenomenon in a 1°

latitude by 1° longitude grid square analysis of a large sample of the Australian flora. The same centres are usually found in different taxa. Conversely, most groups below order or family level have vicariant relatives with maximum diversity, by definition, in different localities.

So for both taxa and characters, nodes may represent the locations of:

- endemism,
- high diversity,
- distribution boundaries,
- disjunction, and
- 'anomalous' absence.

Nodes can be characterized using these five features (Heads, 1990a; Aguilar-Aguilar & Contreras-Medina, 2001; Contreras-Medina *et al.*, 2001, 2003). However, there is more to it than this.

Because of the different levels of genetic potential in different groups, during a given phase of evolutionary modernization in the same region some taxa evolve into new genera, some into new species, some only to the level of cytotypes. Thus the same nodes act as breaks or centres for taxa of different rank. (In dispersal theory and most molecular clock studies, these differing degrees of differentiation are misinterpreted as representing different times or rates of evolution in different groups, or multiple invasions). Finally, not every group is affected at a node – some plants and animals 'pass through' any node with no sign of differentiation.

Below the level of taxa, but above the level of 'no difference', biogeographic nodes often involve character differentiation only. They are also often localities of 'incongruence' where distinctive taxonomic characters can 'drop out'. For example, the New Zealand shrub *Leonohebe mooreae* (Scrophulariaceae) is generally easily distinguished from related species by having stomata on the abaxial leaf surface only. However, populations from Fiordland and NW Nelson have both abaxial and adaxial stomata (Heads, 1992). Another example of incongruence at a node involves members of the plant family Araliaceae. In this group the distinction between inarticulate and articulate flower-stalks has been used to distinguish genera and subtribes. However, flowers of *Polyscias stuhlmannii* var. *inarticulatus* of the Usambara Mountains in Tanzania are inarticulate, although it clearly belongs to a typically articulate group (Tennant, 1960). Some authors have advocated transferring the variety to another genus, *Gastonia*, but this may simply be a case of a node acting as a centre of incongruence.

Thus, nodes are often the localities of:

- incongruence and recombination,
- specimens that are difficult to identify, and
- unusual hybrids.

The legume shrubs *Crotalaria mentiens* and *C. ledermannii* are both narrowly endemic to the Bamenda area of NW Cameroun and were treated together by Polhill (1982). Although their flowers have 'quite different structure', the two species are 'deceptively similar' (Polhill, 1982). In this example, a node (one of four major African nodes; Croizat, 1968) acts as a 'centre of deception'.

Taxa usually have a fairly well-defined altitudinal range, which often becomes lower with increasing latitude. However, altitudinal anomalies often occur. The subshrub *Kelleria dieffenbachii* (Thymelaeaceae) ranges in montane habitats above 400–500 m from New Guinea to SE Australia, New Zealand, and the subantarctic islands of New Zealand, but at Shag Point, New Zealand, it has anomalously low records near sea-level (Heads, 1990a). Other generally montane taxa show the same phenomenon at Shag Point, which is also a centre of endemism for insects (Heads & Patrick, 2003). In addition, the Shag Valley and Waihemo Fault Zone, running inland from Shag Point, is well known as a northern and southern distribution boundary. There has been much uplift and subsidence along the Waihemo Fault Zone which intersects the coastline at Shag Point. Thus nodes can also be sites of ecological (e.g. altitudinal) anomalies.

Nodes are centres of biodiversity and divergence (of monophyletic groups) and also of convergence and parallelism (polyphyly). For example, in the botanically famous SW Cape Province of South Africa, Dahlgren (1971) has illustrated the extensive range of striking morphological parallelisms between the unrelated genera *Cliffortia* (Rosaceae) and *Aspalathus* (Leguminosae).

In another example, the widespread occurrence of myrmecochory (ant-dispersed seeds) in heathland plants of both the Cape Province and Australia represents 'remarkable convergence… across diverse phylogenies' (Bond *et al.*, 1991). These authors noted that 'Ironically, the selective pressures which lead to the evolution of myrmecochory in diverse lineages within the Cape and Australian floras are still enigmatic'. Thus nodes may appear to biologists as centres of enigma and irony.

The problem of 'parallelism' – how and why do unrelated and sometimes geographically widely separated plants or animals sometimes have one or more characters in common? – is only a problem if it assumed that taxa are monophyletic. In centre of origin/dispersal biogeography, characters and taxa are assumed to develop just once, in a monomorphic ancestor – a single parent pair or even a single individual ('Eve') – at a single point and to radiate out from there. In panbiogeography, characters and taxa evolve many times out of a widely distributed, polymorphic ancestor over a broad front, during a phase of regional metamorphism. All taxa are polyphyletic by origin, although they may be monophyletic by evolutionary tendency; the ubiquity of parallelism is a clear indication that the 'same' characters, and thus taxa, can, and often do, evolve more than once.

The most diverse aspects of biological diversity have a spatial structure. For example, 'grotesque' and 'bizarre' forms are often noted by (northern) authors in the biota of Madagascar and south-west Australia. This distribution correlates with a standard track, followed in complementary ways by the presence of monophyletic groups and polyphyletic groups (for example, the group of unrelated plants with 'divaricating' architecture, bearing brachyblasts and long shoots with abortive apices; Heads, 1990b) and also the absence of groups (such as woodpeckers). The bio-spatial structure of the grotesque can be analysed with reference to these Indian Ocean nodes.

In a similar example, the archaeid spiders are among the most bizarre of all spiders structurally, with an enormously elevated cephalic area and grossly developed chelicerae (Forster & Platnick, 1984). They belong to a monophyletic group with five main clades, distributed as follows:

- Archaeidae: South Africa, Madagascar, Baltic amber (fossil), Queensland and Victoria.
- Mecysmaucheniidae subfam. Mecysmaucheniinae: New Zealand, Juan Fernandez, southern Chile and Argentina, Falkland Islands.
- Mecysmaucheniidae subfam. Zearchaeinae: New Zealand, Chile.
- Pararchaeidae: New Zealand, Australia, Tasmania.
- Holarchaeidae: New Zealand, Tasmania.

Here, the 'bizarre' occurs in a southern Indian Ocean/Pacific Ocean group with a thoroughly standard distribution centred on a pivotal node around 'New Zealand' (probably some parts of it rather than others). On the other side of the Tasman Sea, the brilliant but neglected botanist Corréa da Serra (1796) described the 'bizarre' vegetation of Australia as 'Flora at the masked ball' (as quoted by Arber, 1970).

A good example of southern Africa–northern Indian Ocean disjunction was reported by Jeffrey (1988), who noted the 'astonishing geographical disjunction' of *Dactyliandra welwitschii* (Cucurbitaceae): deserts of the Namib (SW Africa) and Rajasthan (NW India). Similarly, on finding a continental Asian moss in Madagascar, Touw (1993) admitted: 'I could hardly believe my eyes'. Thus biogeographic nodes can function as 'centres of astonishment'.

MODES OF SPECIATION IN VICARIANCE AND DISPERSAL THEORY

Nodes are facts of observation, but they have been interpreted quite differently. In dispersal theory, nodes represent centres of origin, or barriers to 'chance dispersal'. In vicariance theory, nodes represent zones, aspects of prior geography around which evolution has taken place. Croizat (1964) compared vicariant form-making with the breaking of a mirror with several blows of a hammer. The sites of the blows are equivalent to the nodes, and the distribution of the pieces of glass, large and small, is because of fracturing, not movement.

The debate between vicariance and dispersal often focuses on whether the physical movement required by 'dispersal' is possible, and on the means of dispersal involved in a particular case. However, these topics are really irrelevant, as panbiogeography accepts both that individual plants and animals move, and that taxa may expand their range. The latter occurs during periods of mobilism, for example around the coasts of the late Mesozoic epicontinental seas. Vicariant form-making cannot take place during periods of mobilism, but occurs during phases of immobilism when large blocks of fauna and flora are relatively sessile (such as the passerine avifauna of today's world). The process of 'chance dispersal' as used to explain evolution is quite different from the ordinary ecological movement by which, for example, a cleared area of ground is soon colonized by populations of pioneer species using normal means of survival. It is a matter of everyday observation that these do not then proceed to evolve into new species.

It is often felt that organisms such as birds 'must' disperse, but the records of distribution, indicating massive endemism and vicariance at all levels, show that this is not true. Wiens (1991) noted that 'because birds are mobile creatures, one might expect the distributional boundaries that define biogeographic patterns to be blurred within continents or biogeographic realms. In fact, many species have quite limited distributions'. Albatrosses roam the oceans, but return to breeding sites that are often very localized and vicariant with those of their relatives (Heads, in press). Many passerines, such as birds of paradise, are highly sessile and individuals may spend much of their lives in a single tree.

The difference between vicariance and dispersal can perhaps be better appreciated not by focusing on 'means of dispersal' but by considering the two as different modes of speciation. Mayr and Croizat have both emphasized that the prevailing mode of speciation is geographical, as in Mayr's 'allopatric speciation' and Croizat's 'vicariance'. However, Mayr (1982, 1997) argued that this occurs in two forms, and 'actually, the two allopatric models are worlds apart'.

In the first model, Mayr's 'dichopatric speciation', a previously continuous set of populations is disrupted by a newly arisen barrier, such as a mountain range or a new arm of the sea, and populations of each sector evolve into a new species over a wide area: there is no centre of origin. In this model earth and life evolve together. In the second model, Mayr's 'peripatric speciation', a founder population is established through dispersal 'by a single inseminated female or by a few individuals' (a clear reference to a Darwinian 'ancestor'). At some point, and somehow (Mayr does not explain how, exactly – chance plays a major role) migration stops and the founder becomes isolated from its parent population. Dichopatric and peripatric modes of speciation are usually known as 'vicariance' and 'dispersal', respectively. [These are not the only synonyms for the same two processes; for example, in anthropology, there is the 'out-of-Africa' model (dispersal) and the 'multi-regional hypothesis' (vicariance) for the evolution of *Homo sapiens*].

Hennig's (1966) German idealist views closely resemble those of Mayr on most important topics. For example, both accept that all taxa derive from single species and both accept (in contrast with Darwin and Matthew) that the 'primitive species' stay at the centre of origin while advanced forms move out. Hennig also accepted the importance of 'peripatric speciation', referring to it as 'speciation by colonization'.

In some of his writings Mayr (1965) seems to accept only peripatric speciation as common and dismisses the importance of dichopatric speciation: 'Quite obviously, except for a few extreme [?local] endemics, every species is a colonizer because it would not have the range it has, if it had not spread there by range expansion, by 'colonization', from some original place of origin'. Here Mayr ignores the possibility of 'dichopatric speciation' involving two or more widespread species, for example, differentiation between north New Guinea and south New Guinea forms, or even a split between a Laurasian form and a Gondwanan form. Most widespread groups show a mosaic pattern, with many genera, species and practically all subspecies showing vicariant ranges. Under Mayr's view, this standard pattern would require a huge number of founding events, point centres of origin, and range expansions, rather than the simple break-up of a widespread common ancestor.

Mayr (1954) proposed his 'peripatric model' ('an entirely new theory of allopatric speciation' – Mayr, 1982) in a paper on New Guinea birds. He introduced the term 'peripatric speciation' in 1982; in 1954 he referred to the idea as the 'founder population' model. The model was based largely on the occurrence of highly 'aberrant' populations of bird species on islands off New Guinea, peripheral to the main distribution, and the 'amazingly great differences' among populations of adjacent islands in New Guinea. Mayr (1954) admitted that 'much' of his paper is 'frankly speculative' but he did not refer to any geology in his study, even speculatively. The distributions he dealt with have been analysed in a very different way in panbiogeographic work (Croizat, 1958; Heads, 2001, 2002), in which models of New Guinea as a geological and biological composite have been discussed fully. These studies concluded that there is no need to invoke 'founder populations' and that massive movements of geological terranes, not 'chance dispersal', account for facts of bird distribution in the region, such as the aberrant populations studied by Mayr and the total absence of birds of paradise from Biak and the Bismarck Archipelago.

The other example that Mayr and many others have based their theories on is the bird *Zosterops* in New Zealand. Mayr (1954) stated that 'a small flock found its way in 1856 from Australia to New Zealand', but this apparently classic example of a founding population is not supported by a closer reading of the literature. Buller (1967) and Mees (1969) have both indicated an earlier presence of this bird in New Zealand and, as ornithology in New Zealand only started at about this time, *Zosterops* may well have been in the country from ancient times, becoming more abundant with the advent of European settlement and agriculture.

In fact, the whole field of founder effects is problematic. Futuyma (1998) has noted that 'founder effect speciation' is 'very controversial' and that 'a great deal of controversy surrounds the genetic changes postulated' for the founder populations in peripatric speciation. Ayala *et al.* (1995) observed that the prevalence of founder events in speciation is a matter of 'acrimonious debate', with some authors rejecting the purported genetic consequences on theoretical grounds. Whittaker (1998) noted that 'it is particularly problematic that founding *events* (i.e. colonization) have been theorized to produce a variety of rather different founder *effects*…(italics in original), and that some authors have queried the significance of founder effects'. Tokeshi (1999) argued that '…despite the conceptual appeal and Mayr's emphasis in his monograph, data which can unequivocally be related to such peripatric speciation are not easy to identify…. Rather than hard empirical evidence of contemporary and historical distribution patterns in faunas and floras, the interest in the peripatric perspective has mainly revolved around its theoretical implications from population genetics. In an attempt to explain the divergence of peripheral populations, Mayr (1954, 1963) advocated the concept of the founder effect… theoretically, however, the founder effect based on random genetic drift does not seem to be an effective means of speciation….' Nei (2002) wrote that while the theory of speciation by the founder principle has been popular for the past 40 years, it is 'speculation, and there has been no empirical study of this hypothesis'. Recent studies of MHC loci in Galapagos finches and cichlid fishes in African lakes, both model cases of speciation by the founder principle, 'led to one of the most important findings in evolutionary biology in recent years: that speciation by the founder principle may not be very common after all.'

Thus, of the two modes of speciation that Mayr himself agreed were 'worlds apart', dichopatric speciation or vicariance is accepted by most authors, whereas peripatric speciation (founder effect, speciation by colonization, 'dispersal') is highly controversial; biogeographers such as Croizat and geneticists such as Nei have simply rejected it.

HOW DO NODES WORK?

The pineapple family, Bromeliaceae, is one of the most abundant and species-rich groups in tropical America, with 1400 species found there in many habitat types – some even grow as epiphytes on power lines. However, the family as such is absent in the Old World tropics, except for one West African species, *Pitcairnia felicis*, on the Fouta Djallon Plateau in Guinea (Hepper, 1968). Richards (1996) concluded that 'the absence of this family in the rain forests of the Old World could perhaps be due to some kind of evolutionary accident'. This is true in so far as the absence is because of differential evolution, rather than ecological factors or long-distance dispersal (or lack of it). However, the absence is no more an 'accident' than any distribution or evolutionary event (perhaps this is why Richards had the phrase in inverted commas). The absence of Bromeliaceae from one sector (the Old World except Guinea) and its presence in another (the New World plus Guinea) is, as Richards (1996) suggested, the result of an evolutionary process. Other than for maintaining the geographic, Wallacean areas (Neotropics, Ethiopian, etc.) there is no special need to invoke any dispersal from the Old World to the New or vice versa, simply the usual widespread, Mesozoic ancestral complex, followed by 'some kind of 'evolutionary accident'. West African plants and animals resembling relatives in the New World, rather than in other parts of Africa and the Old World, is geographically anomalous, but biogeographically is a standard pattern.

WHAT NODES ARE NOT

A node is a location or centre of biological meaning and information, but is not a 'centre' in the Darwinian sense of a simple, original source: a centre of origin. The evolutionary process is often interpreted as a 'radiation', but this concept assumes a morphological and geographic point centre of origin which is not accepted here. Neither are nodes 'barriers to dispersal' – many are not correlated with any geographic barrier. As indicated, nodes are not just centres of presence, but are also distribution margins and centres of absence. Geographically, as a matter of simple observation, most nodes are actually complexes of nodes (e.g. NW Nelson, Fiordland).

Describing the birds of the Solomon Islands region, Mayr & Diamond (2001, p. 249) posed the question: 'Why is the San Cristobal avifauna so distinctive in its endemism, absentees, eastern specialties and differentiation?' They concluded '…some mystery remains and we do not claim to have a complete answer.' They also (p. 254) wrote 'We are uncertain whether these three factors (colonizing ability, wind direction and ecology) suffice to resolve the paradox of Rennell's avifauna…. This paradox deserves more attention.' Finally (p. 229) they referred to the absence of the New Guinea species *Monarcha chrysomela* from New Britain as 'the most surprising distributional gap in the whole Bismarck avifauna' and wrote that the reason for 'its presumed disappearance on New Britain remains mysterious'. They also failed to account for the even more striking absence of birds of paradise from the Bismarck Archipelago. In fact the whole fauna and flora is quite different from that of the mainland.

Do San Cristobal, Rennell and New Britain really represent centres of 'mystery' and 'paradox'? The public always loves a mystery and 'chance dispersal' (favoured by Mayr and Diamond) is inherently mysterious, but outside dispersal theory there appears to be no real reason for accepting nodes as centres of mystery or paradox. Mayr and Diamond did not mention any geological development earlier than the Pleistocene, but this earlier history is probably crucial to a resolution of their mysteries. For example, Hall's (1998, 2001) reconstruction of the region for 30 Ma shows the east Philippines, northern Moluccas and north New Guinea terranes (including New Britain) forming a relatively continuous arc, running parallel with and 1–2000 km north of proto-New Guinea, before moving south and west and docking. This would explain the close connections among these regions and also the great difference between the northern and southern Moluccas, and the Bismarck Archipelago and mainland New Guinea.

Similarly, Rieppel (2002) wrote that the occurrence of groups like chameleons, freshwater fishes and terrestrial mammals in Madagascar 'has been seen as paradoxical' as their origin is assumed to post-date the separation of Madagascar and because they are considered to be poor dispersers. He concluded: 'How chameleons managed to disperse across the ocean must remain a matter of speculation'.

Are nodes refugia? The refugium theory of biodiversity and biogeography, developed through the 1970s, is derived directly from a centre of origin (refugium)/dispersal theory. The refugia are always assumed to be geologically recent, usually Pleistocene, and a critique would elaborate the idea that the main biogeographic patterns, such as the tracks: southern Africa/Madagascar – south-west Australia; or west Africa – Brazil/Guianas, date back to times before the break-up of Gondwana. Most of the 'refugia' proposed by different authors are indeed nodes, but are nodes 'refugia'? The answer must be 'no', as many nodes have not (yet) been recognized by authors as 'refugia', although the number of proposed refugia continues to multiply. In addition, not all nodes are refugia as the usual concept of refugium does not explain nodes acting as both centres and boundaries or breaks in taxa and characters.

WHY NODES OCCUR WHERE THEY DO: NODES AND GEOLOGY

Earth and life evolve together and biodiversity is intimately related to landscape evolution through all kinds of geological and physiographic change. For example, older life may 'float' on younger landscapes as deposition or erosion takes place under the roots and feet of the biota (Heads, 1990a). The withdrawal of inland seas may lead to the stranding inland of previously coastal forms – dispersal by 'sedimentation' leading to distribution in concentric rings (Heads, 1990a,b, 2003, Heads & Patrick, 2003). This is seen clearly in Africa, Malesia, Australia and New Zealand. Croizat (1964) emphasized the spatial correlation of major tracks with major fold belts or geosynclines. In New Zealand and New Guinea nodes have been correlated geographically with zones of terrane accretion, regional metamorphism, belts of granitization and volcanism, faulting and folding, and uplift and subsidence (Heads, 1990a, 2001, 2003). Living communities, like the earth, may also suffer different types of 'erosion' and extinction. Croizat (1958) proposed correlation between biogeographic tracks and the localities of oil deposits. Katz (1968) reviewed the potentially oil-bearing formations in New Zealand, which are all found on epicontinental, unstable shelf areas. He concluded that 'the characteristic lithologic assemblage of possible source sequences is of the shale-sandstone-coal type, and its environment is a transitional one of the near-shore marine and deltaic or estuarine-brackish to freshwater zone… environmental conditions for the formation of bituminous sequences… are often created at the turning points in the paleogeographic history… it is not uncommon for argillaceous sediments lying just above major unconformities to be good source rocks. Rich growth of organic material often took place on land during several periods represented by such unconformities'. It is the nature of this 'rich growth' associated with turning points in paleogeographic history which is of interest to both the biogeographer and the oil geologist.

Marshall (2001) noted that the New Caledonian molluscan fauna in general is 'exceptionally rich' and also cited a 'remarkable' Pleistocene assemblage from Vanuatu. He described the seguenziid gastropod fauna of New Caledonia and found it 'exceptionally diverse', with 91% of the species endemic there. He proposed that 'since the Melanesian arc is situated at current or former (convergent) boundaries of the Australian and Pacific lithospheric plates (subduction zones), species richness there is probably due at least partly to progressive accumulation of taxa transported on the plates'. This process is probably very important and other possible examples can be seen in New Zealand and New Guinea. Tracks can thus develop around subduction zones of the past or the present.

The highest diversity of Neotropical Ericaceae occurs in Antioquia district, NW Colombia (23 genera, over 100 species). This has been attributed to 'adaptive radiation' in the very wet climate there, but a similar pattern occurs in pantropical marine groups, such as fiddler crabs (*Uca*), which also have maximum diversity around the coasts of NW Colombia. This pattern and its occurrence in both marine and montane groups can easily be explained as the result of terrane accretion from the Pacific side (Heads, 2003). In North America, the very high plant diversity in California can likewise be accounted for by terrane accretion.

SURVIVAL AT NODES: LIVING ON, *IN SITU*

The examples cited show that biogeography often reflects the geography and ecology of the past. There may be millions of years of 'ecological lag' and so ecological correlations are primarily with a past, rather than the present, environment. 'Ecological lag' implies a tendency for plant and animal communities to survive, literally to 'live on', where they are, while environmental variables (such as altitude, sedimentation regime and soil chemistry) change with tectonic development. Morphology may also change in an adaptive or non-adaptive way while the taxa remain *in situ*. 'Optimization' arguments in the different fields of biology, such as ecology, are, rightly, much less favoured now than they once were, and the argument followed here does not apply any concept of 'good', 'better' or 'best' to plants or animals and their morphology.

A geographical locus, a sector of the earth's surface represented by geographic co-ordinates, will, through time, experience different altitude, slope, climate, parent material, etc. The plants and animals present will change, of course, depending on the rigours of the environment, from forest, through to woodland, shrubland, grassland and desert. Nevertheless, the taxa of either trees or grasses and their associates, will be drawn from a species pool which is sometimes very local in extent. Even in the oldest and tallest tropical forests there are always smaller open areas, often with surprisingly endemic species. This species pool can expand at any time through the forest zone, for example during periods of climate deterioration. In other words, communities do not really move, there is more like a switching on and off of either the high stress or low stress *bios* already present. In addition, life is often unbelievably 'sticky' and populations may survive on small, ephemeral, ecological 'islands' for long periods of time, for example species of *Ourisia* (Scrophulariaceae; Heads, 1994) and *Pachycladon* (Cruciferae; Heenan & Mitchell, 2003) on 'nunataks' in and around the glaciers of New Zealand. Other examples are terrestrial and reef taxa in the Pacific. Islands such as New Caledonia and Fiji, and even smaller islets, preserve a highly endemic biota. This idea of life surviving on many, small, individually ephemeral sites is fundamental to both panbiogeography and metapopulation theory.

THE AGE OF NODES

Followers of Darwin, Wallace and Matthew have felt that measuring the 'degree of differentiation' among taxa was possible and a valid way of estimating the time of differentiation. This phenetic concept has been adopted by most recent molecular workers, ignoring cladistics' notable advance in the 1970s that showed it to be theoretically awkward, probably irrelevant and certainly unproductive. Wallace theorized that the degree of differentiation is proportional to the time lapsed since the original split, confusing the quite distinct concepts of age of form-making, and time involved in form-making; for example an evolutionary event may have happened very fast, a long time ago. In panbiogeography, degree of difference is taken to indicate neither age of, nor time involved in, differentiation. Croizat proposed that evolution normally works by 'phases of modernization' followed by long periods of stasis. This idea was later appropriated by North American biologists under the term 'punctuated equilibria'.

Dating evolutionary events is discussed elsewhere (M. Heads, unpubl. data). A major logical error often made in molecular clock work involves reference to 'estimated age' of a taxon, when what is actually meant is 'estimate of minimum age' of a taxon, as most calibrations are ultimately based on age of fossils. A group is older to much older than its oldest fossil, and so fossil age is of little use in dating taxa. A better method involves correlating evolution of taxa with spatially related tectonic events. However, this also involves difficulties as activity on tectonic features is often periodically rejuvenated, sometimes over tens of millions of years.

CONCLUSIONS

A biogeographic 'track' is a sector which connects nodes and affinities. The term 'node' means different things in morphology, astronomy, and physics, but the mathematical sense, the point at which a curve crosses itself, and the Latin meaning – 'nodus' means 'knot' – are close to the biogeographical sense of the term.

A typical pattern for three nodes, A, B and C, arranged in a more or less straight line, would involve local endemics at each, breaks in range at each (taxa ranging from A to B and from B to C, or disjunct between these localities), widespread taxa ranging from A to B and C, and occasional cases of 'wing dispersal', with taxa occurring at A and C 'in the wings', but not at B.

Biogeographic regions and their definition have been a major focus of research effort since the time of Wallace and Sclater. Bremer (1993) regarded 'delimitation of areas' as a 'methodological problem' which deserves 'much more attention in cladistic biogeography'. Panbiogeography has instead focused on identifying nodes. Ortmann (1902), for example, writing on Crustacea, concluded: 'It is incorrect to regard the creation of a scheme (of regions) of animal distribution as an important feature or purpose of zoogeographical research. Thus we are justified in saying that zoogeographical study, as introduced by Wallace (and Sclater), is not directed in the proper channels (and results in) fruitless discussions on the limits of the different zoogeographical regions'. Ortmann considered it 'entirely a matter of indifference whether we accept any regions or not', predicting later panbiogeographic treatments of 'biogeography without area' (Henderson, 1990). Instead, 'the chief aim of zoogeographical study consists – as in any other branch of biology – in the demonstration of its geological development'. This is exactly the panbiogeographic approach. Similarly, White (1965) perceived that 'recognition (and naming) of centres of endemism, which may occupy a small or large proportion of the total area of the Domain, and which may or may not overlap with other centres, provides a much truer picture of the chorological pattern than does the division of a Domain into water-tight units'.

Areas accepted more or less *a priori* in biogeographic studies, for example those used in vicariance cladistic analyses, are usually based on geographic areas, are much too large, and are biogeographically and geologically composite. A vicariance cladistic study of the Malay Archipelago, for example, that used areas such as Borneo, Sumatra, New Guinea, would inevitably result in much incongruence (and thus assumption of dispersal). In contrast, a panbiogeographic study of the same area (Heads, 2003, dealing with 800 species of Ericaceae there) recognized none of these areas, but identified many nodes and correlated these with the tectonic history of geological terranes.

The term and concept of 'vicariance' was employed by Croizat through the 1960s as a cornerstone of his panbiogeography and was originally anathema to orthodox biogeographers. Now, however, it appears throughout the literature and even in journals such as *Science*, *Evolution*, *Systematic Biology* and the *Proceedings of the Royal Society*, London. Perhaps the next panbiogeographic term to permeate biogeography will be 'node'.

Reading biogeographic patterns as structured essentially around nodes leads to a consideration of information, meaning and difference in biogeography in general. As shown above, nodes can be centres of endemism, high diversity, distribution boundaries, disjunction, 'anomalous' absence, incongruence, recombination, specimens that are difficult to identify, unusual hybrids, ecological (e.g. altitudinal) anomalies, parallelism, deception, enigma, irony, astonishment, the grotesque, and the bizarre. However, there is no evidence for nodes being centres of paradox or mystery, Darwinian centres of origin, barriers to dispersal, or 'refugia' as in 'refugium theory'.

A node is usually both a centre of presence and also absence, as well as being an edge or break of distribution. In sum, perhaps a node can best be described as a 'place of difference', to use Shakespeare's phrase.

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