What biogeography is: a place for process

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ABSTRACT
The search for understanding of the past and present processes that have and/or continue to generate observed biotic distribution patterns substantially involves historical reconstruction based on present patterns (both phylogenetic and geographical). How this should be undertaken has been a cause for major debate over many decades. Residual patterns do not always provide explicit pointers to the causal processes, and in addition to applying our understanding of earth history, we need also to carefully explore the implications of contemporary processes as a means for unravelling pattern. Some biogeographers assert that earth and life evolve together, but knowledge of distributions and ecologies indicate that this is sometimes true and sometimes false. Just as general patterns may sometimes indicate a commonality of the means that generated the patterns so, too, do observable processes sometimes indicate commonalities. Vicariance and dispersal are fundamental attributes of biotic distributions. Phylogeography has the potential to assist us in determining which of these mechanisms has generated observable patterns.

Keywords
Pattern, process, area relationships, centres of origin, dispersal, vicariance.

INTRODUCTION
Most biogeographers will probably agree with Ebach et al. (2003) that an essential goal of biogeography is to ‘discover why organisms are distributed the way they are today’ (citing Platnick & Nelson, 1978). Moreover, many also agree that this is achieved by uncovering ‘the patterns of spatial distribution attained by life on earth and the means by which these distributions were achieved’ (citing Rosen (1978): 159 [my emphasis]). In both instances, we are looking at the questions of pattern and process. Beyond that, I suspect many will encounter a ‘parting of the ways’ with Ebach et al. (2003), and it is my purpose here to explore some of the reasons for that.

SOME POINTS OF DIFFERENCE
Many will not agree with Ebach et al. (2003) regarding the fact that the essence of biogeography is the determination of area relationships. Area relationships (patterns) are, it seems to me, an (derivative, secondary) outcome of the (primary) processes that generate distribution patterns of individual species, about which, as Ebach et al. (2003) suggest, we are interested in learning. To be sure, part of this process may be about identifying ‘area relationships’, but I think that this is far from the whole picture as Ebach et al. insist. Specifically, I do not accept, as Ebach et al. (2003) put it, that ‘Biogeography is not about finding individual species’ [’] histories (ancestor-descendent relationships and event based scenarios)’ [my emphasis]. Nor do I accept that ‘centres of origin are no longer relevant in explaining general patterns of taxic distribution’ (Ebach & Humphries, 2003). These may not be of interest to Ebach and his colleagues, but they certainly are to me, and a reading of biogeographical papers published in this journal, and elsewhere, gives me the distinct impression that I am far from alone. This is primarily because whatever were the causal mechanisms generating species distributions, the overall patterns we observe are the accumulation of the individual patterns – in a major way, the whole is the sum of its parts. If we do not give attention to individual histories, we face the prospect that varied causations of that history will be subsumed within the general history, and that seems, to me, unrealistic and to lose a great deal from understanding biotic distributions – the implications for understanding process are seriously jeopardized. Sometimes, the parts may show all sorts of similarities, and we are thereby encouraged to search for common causes of common patterns. But there is no fundamental reason as to why these similarities should connect only to geological events, and often, it seems, they may be generated by consistent
meteorological or oceanographic features such as winds and ocean currents, over long time periods. Not only is dispersal sometimes consistent in direction, McGlone et al. (2001) point out that it can be ‘also be a strongly non-random process in that it selects for certain types of propagules and plant types’.

**THE PLACE OF DISPERSAL IN BIOTIC ASSEMBLY**

Contemporary observations tell us that dispersal processes are a key element of the assembly of biotic communities after perturbation, e.g. the oft-cited re-establishment of a biotas on Krakatau, but that is just the easiest and most explicit example (and about which there has been a plethora of papers discussing the contribution of dispersal to re-establishing its biotas from other nearby islands; see Thornton, 1996). The same applies more generally to volcanic islands (see Thornton, 2001). Grehan (2001) joins Croizat (1964) in scorning the mention of Krakatau, and joins those who plead that ‘there is no certainty that all the island’s vegetation was destroyed by the 1883 eruption’ (and by implication, also its animal life). And if they are right, and every last plant and animal was not destroyed, does this negate the massive rebuilding, documented in detail by Thornton and his colleagues? I think not. And if it has been rebuilt, how did it happen if not by transoceanic dispersal? The role of dispersal in re-assembly after perturbation has rather wider implications at more local spatial levels (McDowall, 1996).

Life on the Hawaiian islands is believed to be a broad mixture of biotic elements, all of which arrived there by dispersal process and which connect Hawaii’s biotas to others in virtually all directions (Wagner & Funk, 1995). Some elements are even derived by dispersal from New Zealand, if Wright et al. (2000, 2001) are correct. So, to understand Hawaiian biogeography, we need to look at the processes that resulted in the accumulation of biotas on these islands over several millions of years as the various contributors to Wagner & Funk’s (1995) book do, so elegantly (and see McDowall, 2003). Much the same seems to be true of the Pitcairn group of islands (Kingston et al., 2003), which also comprises a series of relatively young islands that are not considered ever to have had any land connections. Wilkinson (2003) drew attention to similar issues for Ascension, St Helena, Christmas Island and Guadeloupe, and concluded that: ‘Without dispersal, all these islands would be devoid of terrestrial life’. Gillespie (2002) addressed these questions for the Marquesas and Society Islands, based on the fundamental belief that they, like Hawaii, are relatively young, volcanic islands. And she presented interesting (to me, at least) molecular evidence that a particular group of spiders has separately invaded all three island groups by transoceanic dispersal – Hawaii perhaps three times, the Society Islands twice, and the Marquesas just once, providing the foundations for the evolution of endemic species on islands of all three groups. Interestingly, Gillespie (2002) argues that the sources of the dispersants for each island group are varied, including North America, the Caribbean, Australia, and even as far away as Indonesia. Despite these varied sources, the suggested derivations create a repeated pattern of invasion and speciation, even to some extent accumulating to a general one. Cox (1998) chose another group of islands listing, in addition to some of the above, Line Islands, Tuamotus, Cook-Austral, Samoa, Marshall-Gilbert-Ellis, Aleutians, Kuriles, Isu-Bonins, Marianas, New Britain, Solomons, Tonga, Kermadecs, and concluded that ‘the biotas of all these Pacific islands are due to overseas dispersal’. Moreover, he points to impoverishment of island floras, moving from west to east, and biotas, which ‘contain a high proportion of organisms that can easily arrive by air’. Wilkinson (2003) drew attention to the fact that microorganisms ‘are so small and numerous that they can disperse anywhere’, as a result of which they tend to be cosmopolitan. These taxa, like oceanic islands, are at extremes of taxic (geographical) continua. Interestingly, Ebach and Humphries do not seem to invest much effort in vicariance theories for the biogeography of albatrosses or oceanic sharks. And what of ferns, which seem to have massive capacity for spread (Wolf et al., 2001). What we are seeing, of course, is that we can explore ‘all over the place’ both taxonomically and geographically, and find taxa or places where it seems inevitable, or inescapable, that dispersal plays a major role in the development of patterns. Wherever we look, ‘cracks’ appear in the ‘only vicariance’ edifice. I share Wilkinson’s lament that ‘A theoretical base for biogeography that was inapplicable to such fascinating islands [as those mentioned above]…would be sadly lacking’. And, I agree with his closing comment that ‘Darwin (1859) may have showed great good sense in emphasizing the importance of dispersal, not merely because he did not know about plate tectonics, but because dispersal is a fundamental process in understanding much of biogeography’.

Ebach et al. (2003) may also choose to reject molecular evidence and phylogeography, and the extent to which that evidence points to the occurrence of dispersal, but for other biogeographers these disciplines are both informative about phylogenetic relationships and in providing some ability to place dates on genetic/reproductive connections between isolated populations of taxa, and only dispersal can provide acceptable mechanisms of derivation for many of these. Authors like Ebach et al., who prefer generally to ignore or deny dispersal, may point to all the oceanic islands listed above as being remote and therefore somehow different or abnormal, but if animals and plants can disperse to them, as it seems they have, why can they not also disperse to other lands where there also seems to be a role for other mechanisms of derivation. These remote islands are ‘different’ in the nature of their isolation, but surely the processes involved in the derivations of their biotas are subsets of the processes that operate globally, at least in part.

**AREA RELATIONSHIPS AND THE BIOGEOGRAPHY OF REMOTE ISLANDS**

Following Ebach et al.’s (2003) dictum, the biotas of the islands that I discussed above (Hawaii, Pitcairn, Society...
Islands, the Marquesas, Christmas Island, Guadeloupe, etc.) would seem to have no ‘area relationships’ at all as their biotas seem to be derived by complex and varied dispersal processes, over millions of years, and from diverse directions. Does this then mean that these islands have no ‘biogeography’? Or if they do have a biogeography, and all biogeography consists of ‘area relationships’, as Ebach et al. demand, what are these area relationships, and what do they mean in terms of the essential question of ascertaining the processes that produced the patterns that Ebach et al., insist ‘is’ biogeography?

The Falkland Islands biota is almost exclusively one of Patagonian affinities. Does this, then, reflect an area relationship (as Heads, 1999, has argued for the plant genus Abrotanella and Craw, 1988, for Hebe elliptica)? Such a Patagonia–Falklands area relationship would be really fascinating, because in terms of geological history, the land mass constituting the Falkland Islands is believed to have broken away from the south-eastern corner of South Africa, and to have then rotated across the southern Atlantic until it parked up against Patagonian South America (Marshall, 1994; Richards et al., 1996). Where are the indicators of Falklands ‘area relationships’, and what is the meaning of an ‘area relationship’ between Patagonia and the Falkland Islands based on their shared biotas – given that the Falklands were formerly part of south-eastern Africa? Moreover, where are the biotic elements that reflect that ‘area relationship’ that indicate the Falklands’ former African connection? What does panbiogeography have to say about earth and life evolving together, with regard to Falklands–Patagonian biotic affinities?

NEW ZEALAND BIOGEOGRAPHY AND ITS AREA RELATIONSHIPS

The above are, of course, the relatively simple and clear-cut scenarios for interpreting biotic origins and relationships. Geological evidence shows that proto-New Zealand became detached from Gondwana many millions of years earlier than did Australia and South America (Cooper & Millener, 1993; Swenson et al., 2001). One would expect that these timings would reflect its ‘area relationships’, and they probably do in many instances, i.e. that Australia and South America would have stronger joint area relationships in their biotas than Australia and New Zealand do (Brundin, 1966). Yet, the biotic connections between Australia and New Zealand across the Tasman Sea (c. 2000 km) are legion – much more numerous and clear than any connection between Australia and Patagonia. Some relationships clearly connect New Zealand and Patagonia, without an Australian involvement. What then are New Zealand’s ‘area relationships’? From its geological history there ought to be area relationships between New Zealand and Australia + South America. There are, of course, such connections, but there are also some close [New Zealand+ South American] connections (Sykes & Godley, 1968; Hurr et al., 1999; McDowall, 2002).

Given all this, what are we to make of New Zealand’s biogeography, if all biogeography is to be based on ‘area relationships’? New Zealand’s situation seems unlikely to be as inherently ‘simple’ as seems true of Krakatau, Hawaii and the Falkland Islands, because of its much more convoluted geological history both in terms of former continental connectedness and its present isolation. There is strong evidence that much of New Zealand’s terrestrial bird fauna has arrived in the past 1–2000 years (Worthy & Holdaway, 2002). If we are interested in discovering the processes (‘the means by which these distributions were achieved’, as Ebach et al. agree), we have the processes taking place before our very eyes. The question is to what extent does what is happening now indicate past history, and/or to what extent is the knowledge of birds apply to other taxa? I question the insistence by Ebach et al. that our understanding needs to be based on a dependency on pattern (area relationships) – a relatively indirect pathway to clarifying relationships and pointing to processes. Humphries (2000) addressed some of these questions in a paper entitled: ‘Space, time, form: which came first?’, and it seems to me that he asked the wrong question, or at least asked an inadequate question. Process comes first, and pattern is its outcome.

Much of the likely substantial role in the derivation of the New Zealand biota from Australia seems to be by dispersal (Fleming, 1979; Pole, 1994). In the view of some New Zealand botanists this is virtually unarguable (McGlone et al., 2001). If we look more broadly at New Zealand’s biota it is clear that some elements are very recent arrivals – not just birds as mentioned above, but also diverse insects and lots of plants – arrivals predictable with certain well-recognized weather systems such as strong westerly moving weather systems, often associated with forest fires in eastern Australia causing massive updraft and carrying animals and plants with it. Although formerly present only in Australia and islands to the north, even a diadromous freshwater fish has recently begun arriving in New Zealand (McDowall et al., 1998). There is absolutely no reason why the relationships ‘should be chaotic, wide-ranging and pattern limited’, as McCarthy (2003) argued. Molecular evidence suggests that various biotic elements have had gene flow between Australia and New Zealand during late Tertiary times – distributions that parallel the recent arrivals in direction and their area relationship. Chiswell et al. (2003) argue that recruitment of juveniles into the rock lobster fishery in south-western New Zealand may actually originate from Tasmanian reproduction across the Tasman Sea – same processes, different dates.

Some apparently ‘ancient’ elements in the New Zealand biota seem likely to date back to Mesozoic times, and perhaps do express an area relationship also involving Australia and South America, and thus Gondwana – Agathis, hyridellid mussels, parasacid freshwater crayfishes, Peripatus and Sphenodon. Some would also mention Notohagias. Winkworth et al. (1999) add plants from the families Proteaceae, Podocarpaceae, Winteraceae and terrestrial gastropods as possibly of Gondwanan provenance. Daugherty et al. (1993) provide another overlapping list of various taxonomic groups. But area relationships among Australia, South America and New Zealand must be complex.
Zealand would probably be inconsistent – involving various couplets among this triad, depending upon which group was being examined and how their distributions developed. It seems clear, to me at least, that in some, perhaps many, instances, various related taxa exhibit what seem to include both ancient Gondwana relationships and more recent dispersal connections (see Swenson et al., 2001; Swenson & Hill, 2001, for discussion of this in Nothofagus). Emerging evidence indicates the same for the southern cool temperate galaxiid fishes – some groups of which appear to have relatively recent dispersal origins in New Zealand (Waters et al., 2000), whereas others may be more ancient, and are perhaps Gondwanan (McDowall, 2002; McDowall & Waters, in press).

A recent paper on the biogeography of the plant genus Gunnera is both interesting and relevant. Wanntorp & Wanntorp (2003) describe a distribution pattern largely relating to vicariance events, in some instances implicating an evident former Gondwana connection. But there are species in Hawaii and if conventional wisdom about the history of the Hawaiian biota is correct (Wagner & Funk, 1995), it has to be a result of dispersal, raising several issues as given below.

1. There must be multiple explanations for observed distribution patterns.
2. If Gunnera could reach Hawaii by dispersal mechanisms, there is a probability that other parts of the global distribution of the genus could equally result from dispersal, but how much and how do we choose remains a question.
3. Their evidence of phylogenetic relationships in some instances shows closer connections between Australia and New Zealand, than between Australia and South America, a pattern that Wanntorp & Wanntorp (2003) recognize ‘is in conflict with biogeographic studies based on insects’ (citing Brundin’s, 1966 studies on chironomid midges), and with the geological history of the southern hemisphere.

These sorts of multiple explanations for biogeographical connections should not be regarded as unusual; they are probably routine.

SOME BIOGEOGRAPHICAL CONTINUA AND NEW ZEALAND BIOGEOGRAPHY

It seems that there is a huge temporal biogeographical continuum, at one end of which there are contemporary arrivals that are clearly dispersant, some unarguably so. If we look further back in time across that continuum, we might imagine reducing confidence in the view that various elements express an Australia–New Zealand connection that derives from dispersal (although molecular evidence would in my view be helpful here; Ebach et al., 2003 seem to think otherwise). At the other end of that temporal continuum are groups that are widely accepted as probably expressing an area relationship involving some or all the lands that formerly constituted Gondwana (Daugherty et al., 1993; Winkworth et al., 1999). If we could look forward across this temporal continuum from the time of Gondwana, there would be at least some biogeographers who would have growing doubts regarding the fact that the distributions of group are an expression of such ancient area relationships.

Interestingly, I believe, there is also a parallel spatial vicariance/dispersal continuum. At one end of this continuum, there are clearly biotas, typically on highly isolated, oceanic islands, often volcanic and generated by mid-oceanic volcanism that have never had any known land connections (Hawaii, Pitcairn, Society Islands, Marquesas, to list a few mentioned elsewhere in this paper). For these the biota is equally clearly a product of species dispersing, becoming established, undergoing phyletic evolution and sometimes lively diversification, and thus ‘growing into’ endemic island biotas. At the other end of this continuum are large, ancient, stable continental blocks of land that have fragmented under the influence of plate tectonics, provoking vicariant speciation processes, generating endemic biotas and providing the basis for Ebach et al.’s (2003) ‘area relationships’. I suspect that there are very few biologists who would contest either the dispersal or vicariance explanations at the extremes of this continuum, although it seems Ebach et al. would. However, between these two extremes are lands that probably had former continental land connections that became fragmented by plate tectonic processes, and which carried with them fragments of the former continental biota. These old elements would have undergone vicariant speciation processes and have developed into a biota peculiar to that land, and would also have suffered extinctions, under the influence of changing climates and biotas. In addition, such now isolated land areas will have received influxes of additional biotic elements, dispersing from ‘up-wind’ or ‘up-current’, often giving the appearance of being a biota derived from some other, more or less distant source biota. The relative contributions of the vicariant and dispersal contributions to the continental island’s biota will have varied through time and according to the characteristics of the island biota, climate, geology and other effects.

Let us consider a scenario, which is believed to apply to New Zealand, in which the early biotic history of an area implicates habitat continuity resulting from Gondwanan land connections, but that land area moves, breaking the Gondwana connection; a later, prolonged biotic history implicates dispersal, which is, not surprisingly, most obvious recently. Then, in such a circumstance, there will be a shift from the early predominance of vicariant speciation events of an ancient biota of that area, to an increasingly dispersal-derived biota, as the older taxa are affected by extinction and/or are replaced by incoming dispersants.

Although we may have considerable assurance that biotic elements at the two ends of both of these temporal and spatial continua may express either ancient area- or recent-dispersal relationships, there is a vast array of biotic relationships between these extremes for which we do not have much assurance at all, as to the processes behind the patterns. Separating which biotic elements might have ancient vicariant origins from those that have dispersed more recently will depend on contributions from various disciplines.
The discovery of dateable fossils will certainly help by placing a minimal time back to the taxon’s presence in an area (although absence of fossils will have limited value). In addition, this is a field where molecular evidence and phylogeographical analyses can have significant contributions by providing estimates of time-scales since latest gene flow (Avise, 2000). This situation may leave us with all sorts of uncertainties that Ebach et al. find uncomfortable or unsatisfactory. If so, then that is the nature of the ‘beast’ we call biogeography. For me any greater assurance based on dogma is even more uncomfortable or unsatisfactory.

Considering a broad perspective: Why should we depend on biogeographical interpretations, based on area relationships that are derivative, when some of the sorts of processes we seek to understand are taking place ‘right under our noses’? And how are we to distinguish what might seem to be area relationships from congruent patterns that derive from consistent dispersal processes? For Ebach & Humphries (2003) and Ebach et al. (2003), the dispersants among the faunal elements just disappear within a commitment to area relationships; maybe for them they are just noise (but if so it seems very loud!).

If recent, observed biotic connections can be attributed to recent dispersal, and in lots of instances it seems that they can, how are we to know whether:

1. what seem to be slightly older biotic connections are really a reflection of area relationships as Ebach et al. would insist, or whether,
2. they are, or some of them may be (and if so how many?), a product of parallel dispersal events for which the passage of time has resulted in morphological and molecular divergences.

Ebach et al. (2003) and others, seem locked into explaining all biogeography in terms of earth history, and seem either unaware, or are unwilling to admit, that patterns of waif dispersal although perhaps stochastic in timing, may be surprisingly regular and enduring in source, direction and target areas. And this regularity may generate patterns of distribution that resemble vicariance patterns in general appearance and/or may also be congruent with those vicariance patterns. Where then do area relationships enter the scene and to what extent?

WHERE TO, THEN, FOR BIOGEOGRAPHY?

Ebach et al. (2003) ask, seemingly frustrated and, one may suspect, rhetorically: ‘Will there ever be a ‘whole’ biogeography?’ Perhaps not, as resurrecting the details of ancient history will always have uncertainties, but phylogeographical studies will certainly help. Moreover, I have serious doubts that the approach adopted by Ebach et al. provides any greater clarity, certainty or long-term stability of view. But, most of all, there is a need for a pluralistic approach (as evident in Swenson et al., 2001 and Wanntorp & Wanntorp, 2003).

Humphries (2000) found it ‘hardly surprising’ that Tassy & Deleporte (1999) described historical biogeography as being in ‘a mess, a subject looking for a method’, and that remark was made in his critique of the diversity of methods used by historical biogeographers. I think that both Humphries and Tassy and Deleporte were wrong – diversity is a great strength of biogeography (and makes it much more fun). Moreover, despite Ebach et al. (2003) calling phylogeography ‘insular and blinkered’, I have no doubt that its past contribution to historical biogeography has been immense (Avise, 2000), and that it will continue to be. Finally, I reject Ebach et al.’s intolerance of the use of diverse approaches to understanding biotic distributions. I think that there is a fundamental difference between the ultimate goals being pursued by Ebach and his colleagues, in comparison with those whose work they criticize. Ebach et al., it seems, are interested in identifying overarching biotic relationships (patterns), and I have no problem with that. For others, there is a fascination in understanding the diverse ways that biotas have developed, both spatially and temporally through global history (processes). For me, as must by now be clear, the second goal is much the most interesting.

If the identification of area relationships has a contribution in elucidating and illuminating ‘why organisms are distributed the way they are today’ (Platnick & Nelson, 1978), it has to be on the basis that the distributions of species are relatively stable in evolutionary and geological time. If that is so, then it seems to me that over the past 50 years, biogeography has metamorphosed from:

• an approach that had continental positions and relationships stable, with animals and plants ‘dispersing all over the place’, to
• one where animal and plant distributions are stable, and land masses are ‘dispersing all over the place’.

I find neither approach better or worse than the other. Ebach & Humphries (2003) consider that ‘A rationale for biogeography is that Earth and life evolve together’ (Croizat, 1958, 1964), but the problem is that they both do and they do not. There is no single, inclusive explanation of biotic distributions as simple as ‘earth and life evolving together’. All these are half-truths and need to be recognized as such. Enduring hypotheses are likely to be those framed within broad conceptual approaches to biogeography.

REFERENCES


R. M. McDowall has spent most of his career working on the systematics and relationships of fishes of the southern cool temperate zone, and has had a long interest in processes that influence the distributions of life in southern lands.