

BOOK REVIEW

A WORLD SHAPED BY MIRACLES

***The Monkey's Voyage: How Improbable Journeys Shaped the History of Life.* Alan de Queiroz. 2014. New York: Basic Books, 370p.**

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The main theme of de Queiroz's (2014) book is that an irrational school of thought, vicariance theory, dominated biogeography from the 1970s to the 1990s, but that a new theory, chance dispersal, subsequently reclaimed the field. The reality is somewhat different. From the rise of the neodarwinian Modern Synthesis in the early 1940s until now, chance dispersal has been the dominant paradigm in biogeography, and its supporters have occupied all the senior positions in the field. Nevertheless, vicariance began to be taken seriously in the 1970s, and since then it has become widely accepted despite its radical undermining of the traditional theory (Fig. 1).

In this review, 'DeQ' refers to de Queiroz (2014); numbers cited in brackets refer to page numbers in the book.

An earlier review of DeQ's book concluded: 'as a history it is sadly incomplete...', the author 'takes most second-hand stories at face value...', and 'the book takes a sometimes uncritical look at its subject' (Morrison 2014). This uncritical attitude also characterizes much modern biogeography; authors adopt a 'plug-and-play' approach, running their data through popular programs and accepting the results without question.

DeQ's book glosses over any inconvenient evidence, and this is most obvious in the fact that distribution maps are almost entirely absent. In the first sentence, DeQ writes that he recently put up a map of the world in his house for the children; 'As something of a map hoarder... I appreciate a map made with

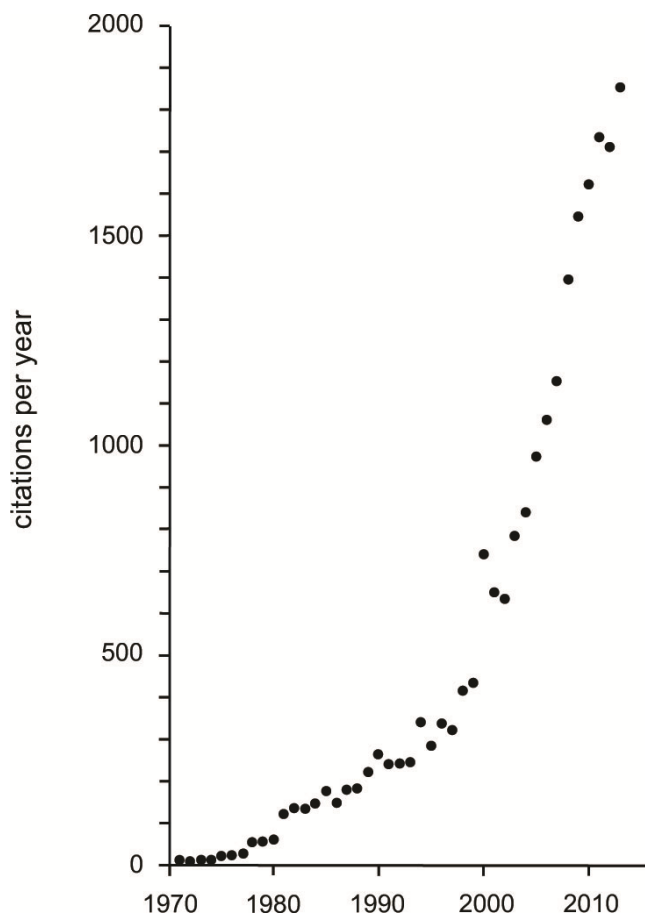


Fig. 1. Number of citations of 'vicariance' per year (Google Scholar, accessed 20 July, 2014).

care...' (1). The map he put up on his wall showed different groups (lions, kangaroos, etc.) in their respective areas. Some of the main evidence for vicariance theory consists of distributions and their surprising repetition in large numbers of groups, and this is best depicted in maps. The one that DeQ put up for his children is an excellent example. Nevertheless, despite his book including dozens of figures illustrating famous personages, organisms, phylogenies etc., there is only one distribution map (Fig. 1.2), showing a snake that the author studied in northern Mexico. The book focuses on intercontinental distributions and continent/island distributions, so why are there no maps showing the details of these? Maps, as with any graph, allow the facts to speak for themselves, so why is any engagement with the key evidence avoided in this way?

VICARIANCE AND DISPERSAL

DeQ correctly distinguished between two forms of dispersal that are often confused (10). *Normal dispersal* is seen every day, for example, in the weeds colonizing a garden, or an albatross crossing an ocean, and it is made possible by a group's normal, observed means of dispersal. This process does not lead to speciation.

The second process is *chance dispersal* or founder dispersal (it is often termed 'long-distance dispersal' [LDD], although it may occur at any spatial scale). This is proposed as a mode of speciation that involves one-off dispersal events 'across a barrier' by a founder. It may only

occur once in the entire history of a lineage, and it does not rely on the group's normal means of dispersal (these are 'not informative in the context of LDD'; Higgins et al. 2003). Chance dispersal is the basic concept of modern dispersal theory (LDD as used by ecologists is simply normal dispersal over long distances, with no implication of speciation.; as used by biogeographers and systematists, LDD is a mode of speciation).

A third, key concept is *vicariance*. In this process, allopatric species differentiate following the development of a *new* geographic barrier within the range of a widespread ancestor. This contrasts with speciation by the chance dispersal of a founder across an *old* barrier. Vicariance was the basic concept of Croizat's (1958) panbiogeography, a synthesis of plant geography, animal geography and geology that gave rise to modern vicariance theory.

Dispersal theory and vicariance theory attribute speciation and allopatry to chance dispersal and to vicariance, respectively, but agree that overlap is caused by normal dispersal (Table 1).

In a founding document of modern dispersal theory, Darwin (1859: 352) wrote that:

Undoubtedly there are many cases of extreme difficulty in understanding how the same species could possibly have migrated from some one point to the several distant and isolated points where now found. Nevertheless the simplicity of

Table 1. The differing explanations for allopatry and overlap as given by dispersal theory and panbiogeography/vicariance theory.

	Explanation for allopatry	Explanation for overlap
Dispersal theory	Chance dispersal	Normal dispersal
Panbiogeography and vicariance theory	Vicariance	Normal dispersal

the view that each species was first produced within a single region captivates the mind. He who rejects it, rejects the *vera causa* of ordinary generation with subsequent migration, and calls in the agency of a miracle.

Thus, in dispersal theory, all species have had a localized centre of origin; if a species or a higher-ranked group occurs in two places, it must have dispersed from one to the other (27). In this model, vicariance is rejected. In a very influential text, Matthew (1915) supported Darwin's model, and a century after Darwin's book was published Mayr (1965) wrote: 'Quite obviously, except for a few extreme [i.e. 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'.

In a later discussion of speciation, Mayr (1982) wrote that while some textbooks showed 'a widespread species cut in half by a geographical barrier', 'more detailed studies... suggest a different solution', namely speciation by

founder dispersal. The widely-used text-book by Stebbins (1966, Fig. 5-1) agreed with Mayr. It showed allopatric differentiation developing solely by migration and ecological differentiation; there is no mention of the appearance of new barriers. In other popular text-books on speciation, Grant (1971, 1981, 1985) included many maps of allopatry, but did not mention geographic change as a mode of allopatric speciation. In contrast with these texts by Mayr, Stebbins and Grant, most text-books written after the mid-1980s cite vicariance as one of the main modes of speciation.

In dispersal theory, a widespread species achieves its wide range by dispersing, often over isolating barriers that *already* exist, and these barriers will then lead to isolation. The dispersal over the barriers takes place by chance dispersal of one or a few founders. In vicariance theory, the *formation* of the barriers leads to allopatric differentiation, other words, Earth and life evolve together.

Areas of high species diversity, such as central New Guinea or the Andes, are often

located in areas with many potential barriers. In dispersal theory, the species (founders) have dispersed over the barriers, and the founder effect has produced the new species. In this model, Earth and life do not evolve together. In vicariance theory, the barriers have developed, by uplift, subsidence and so on, dividing the earlier species in the region and leading to the formation of new ones.

Modern authors such as Eldredge et al. (2005) agreed with Mayr: 'Novel forms must spread beyond their site of origin if they are to have a reasonable chance of being preserved in the fossil record'. But in the case of, say, a world-wide group differentiating into northern hemisphere and southern hemisphere clades, both groups are already widespread at the time of their origin.

DeQ also assumes a centre of origin. For example, he writes (153): 'Over millions of years, members of the genus [the sundew, *Drosera*] obviously have moved great distances, as their world-wide distribution indicates...'. *Drosera* is sister to *Dionaea* (east coast of the US) and *Aldrovanda* (Old World, but absent from most parts of Africa, Asia and Australasia) (Rivadavia et al., 2003). Thus, if *Drosera* originated by simple vicariance with its sister group, it could have already been widespread globally (absent only from east coast US and parts of the Old World) at the time of its origin.

As DeQ writes, vicariance biogeography emphasizes fragmentation (vicariance) events (13). But it is obvious that vicariance cannot be

the only process leading to distribution; vicariance on its own would result in every small area on Earth having only one, endemic clade. During phases of mobilism, groups expand their range as the result of geological or climatic change, and this leads to clade overlap. During phases of immobilism, groups can undergo vicariance, resulting in allopatry. DeQ seems to understand this and he cites phases of immobilism and mobilism (81). Nevertheless, he ends all his chapters with examples of observations on animals and plants moving long distances, as if this indicates chance dispersal; 'we know that long-distance dispersal occurs because people have actually seen it happen' (228). But this is normal dispersal (without speciation), which often occurs over very long distances, as in albatrosses, sharks, migrating birds etc., and is observed by sailors every day.

One important implication of vicariance is that the development of a barrier – a new seaway or a new mountain range, for example – will affect not just one group, but many groups in the community. Thus it is a potential explanation for biogeographic patterns, which are typically repeated in many groups and are not easily explained by chance dispersal.

THE MYTH THAT DISTRIBUTION IS CHAOTIC

DeQ cites 'serious weaknesses in Croizat's argument... First, his claim that there are very few fundamental tracks was misleading. The tracks of individual lineages on New Zealand, for instance, run all over the place – to New Guinea, New

Caledonia, South America, Australia, Tasmania, and Southeast Asia, among other places.’ (82). Obviously, if affinities are traced far enough, all areas eventually connect with all other areas. But with respect to direct connections, there is a common one linking New Zealand to New Guinea, but not to Southeast Asia (either the mainland or, for example, the Philippines); to north-eastern Australia, but not to north-western Australia; to Madagascar, but not to India; to southern Africa and East Africa, but not to West Africa, and so on. DeQ also cites direct affinities of Hawaiian groups linking the islands with different parts of the Pacific margin. But there are no standard tracks linking Hawaii with Europe, India, or Brazil, for example, and all of these would be well within the range of chance dispersal.

Considering phylogenetic and biogeographic breaks (nodes), it is well known that these are concentrated in particular areas. Wallace’s line is perhaps the best known, but there are many others; some involve very large numbers of groups, while others are of more local significance and involve fewer, lower-ranked groups.

If distribution patterns did indeed ‘run all over the place’ and were chaotic, there would be no point in studying them. This is the fundamental message of dispersal biogeography, and it is this nihilist approach that has led to the surprising lack of distribution maps in many biological ‘monographs’ (in contrast, a geological monograph of a region without maps is

inconceivable). Seeing distribution as the result of chance effectively short-circuits a science of biogeography; for any distribution, an author simply concludes: ‘it must have been caused by a chance dispersal event achieved by unknown means’, and that’s it. Much less work is involved, as there is no need to understand the complicated geology of the area, or compare the distribution with a large number of others in the same area to see if it conforms to a standard pattern.

CONCLUSIONS

At the end of his book, DeQ adopts an apocalyptic tone, citing plagues of locusts (280) and presenting a summary chapter titled ‘A world shaped by miracles’. For DeQ, dispersal works by miracles, and this is the only possible view: ‘...it *must* be that the living history of the entire planet has been deeply influenced by ocean crossings and other long-distance colonizations. That is an *inescapable* conclusion ... Chance colonizations have had *clear* and profound effects...’ (296); ‘By now it should be *clear* that, for a large number of [transoceanic disjunctions] ... the primary explanation of the vicariance biogeographers – ...drifting tectonic plates – was the wrong explanation’ (281). [Emphases added]. But all this can be justified only by relying entirely on the clock dates, and if they are wrong the evidence for the miracles melts away.

For DeQ, the basis of biogeography is a mystery and a miracle: the unanalyzable chance event, that, given enough time, becomes a

certainty. No-one is denying that extremely rare events occur, but vicariance theory suggests that it is the norms and averages of biological and geological processes that have shaped the world, not miracles. One of the problems with miracles is that they can explain anything at all. Chance dispersal is not related to any other phenomena, either physical or biological. In contrast, normal dispersal follows laws of probability, and is related to measurable physical parameters such as wind direction, currents, and measurable biological parameters such as a group's observed means of dispersal.

Trewick and Wallis (2001) and McDowall (2008) have criticised panbiogeography for being concerned with general patterns and not accepting the lawless, one-off events of long-distance founder dispersal. Likewise, in the seventeenth century, good theologians such as Bossuet criticised the early scientists and sympathetic philosophers for their dangerous belief in 'general laws' of nature, as this was incompatible with the existence of miracles. In the middle ages, as in modern dispersal theory:

There was proof by miracle as well as proof by authority... What made medieval minds agree to believe in something was not what could be observed and proved by a natural law or by a regularly repeated mechanism. On the contrary, it was the extraordinary, the supernatural or at least the abnormal. Science itself was more willing to take as its subject the exceptional, the *mirabilia*... (Le Goff 2001: 329).

Since the 1970s, several components of vicariance theory have become much more widely accepted. From the 1940s to the 1980s, one of its key concepts, vicariance, was almost completely suppressed by authors such as Mayr, Stebbins and Grant in widely-used text-books (see above). Thanks to the work of Croizat et al. (1974) vicariance was introduced to the mainstream, and it is now well-established (Fig. 1). Associated concepts of vicariance theory – that Earth and life evolve together, that fossils only provide minimum ages, and that many species are older than the Pleistocene – have also become familiar. In contrast, other aspects of vicariance theory, such as the rejection of chance dispersal as a mode of speciation, have not yet been accepted. But the retention of chance dispersal is largely based on conservative prejudice and hold-overs from the Mayrian approach. These are seen in 'ancestral area' programs that automatically find a centre of origin (at the locality of a basal paraphyletic grade), and in the illogical treatment of fossil-calibrated clock dates as maximum clade ages or close to them.

DeQ admitted that vicariance theory is 'inherently attractive' and 'seductive' (269), and this is supported by the evidence that DeQ cites, as well as the evidence he overlooks. DeQ also admitted that random dispersal is 'ugly' (272). This is because it relies on a literal reading of the fossil record; on molecular studies that illogically convert minimum clade ages into maximum ages; on the suppression of critical evidence (such as distribution maps); and on the use of chance and

'miracles' to explain clear-cut patterns that are repeated in many groups.

Despite making these admissions, DeQ concluded that dispersal theory is not only corroborated, but is the final answer for biogeography. While the debate between chance dispersal and vicariance has been a long one, DeQ wrote that '...we're finally getting it right' (268). Molecular dating is 'the final step that might finally produce a paradigm in historical biogeography' (276), and 'It strains credibility to simply dismiss it [molecular dating] as some sort of misguided intellectual fashion... Certainly, many mainstream scientists now see the rejection of the molecular clock as irrational' (277). Yet no one has ever suggested this in print, and many mainstream scientists (such as Morrison 2014, quoted above) have instead given reasons to suspect that molecular clock dates could be seriously flawed.

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