Metapopulation vicariance explains old endemics on young volcanic islands

Michael Heads*

Buffalo Museum of Science, 1020 Humboldt Parkway, Buffalo, NY 14211-1293, USA

Accepted 20 March 2017

Abstract

Terrestrial plants and animals on oceanic islands occupy zones of volcanism found at intraplate localities and along island arcs at subduction zones. The organisms often survive as metapopulations, or populations of separate sub-populations connected by dispersal. Although the individual islands and their local subpopulations are ephemeral and unstable, the ecosystem dynamism enables metapopulations to persist in a region, more or less *in situ*, for periods of up to tens of millions of years. As well as surviving on systems of young volcanic islands, metapopulations can also evolve there; tectonic changes can break up widespread insular metapopulations and produce endemics restricted to fewer islands or even a single island. These processes explain the presence of old endemic clades on young islands, which is often reported in molecular clock studies, and the many distribution patterns in island life that are spatially correlated with tectonic features. Metapopulations can be ruptured by sea floor subsidence, and this occurs with volcanic loading in zones of active volcanism and with sea floor cooling following its production at mid-ocean ridges. Metapopulation vicariance will also result if an active zone of volcanism is rifted apart. This can be caused by the migration of an arc (by slab rollback) away from a continent or from another subduction zone, by the offset of an arc at transform faults and by sea floor spreading at mid-ocean ridges. These mechanisms are illustrated with examples from islands in the Caribbean and the Pacific. Endemism on oceanic islands has usually been attributed to chance, long-distance dispersal, but the processes discussed here will generate endemism on young volcanic islands by vicariance.
© The Willi Hennig Society 2017.

Introduction

"Plate tectonics, perhaps more than any other phenomenon, has had profound effects on the biogeographic patterns of both terrestrial and marine biotas" (Lomolino et al., 2010, p. 306).

For many years biologists assumed that plant and animal taxa attained their distributions by physical movement away from a centre of origin. Until the 1970s, few authors accepted that vicariance—the subdivision of widespread ancestral biotas—could generate diverse, widespread clades. Instead, most biologists argued that barriers acted to isolate clades because of the rarity of chance dispersal across them, not by the formation of the barriers themselves (review in Ebach and Williams, 2016).

Vicariance became more widely accepted through the 1970s and 1980s, but many biogeographers assumed that it could operate only on continents, as the result of continental breakup or the uplift of mountain ranges. Now, in the molecular era, most authors accept that vicariance occurs in many different geographical contexts and at a wide range of scales. However, vicariance is still not accepted as an explanation for the classic exemplars of evolution—endemic land organisms on young volcanic islands and archipelagos. This paper suggests several ways in which vicariance could account for these.

Metapopulation theory

Most species, whether on continents or islands, have distributions that are patchy and located in discontinuous areas of suitable habitat. These species each exist

*Corresponding author.
E-mail address: m.j.heads@gmail.com

as a metapopulation, that is, a population of distinct sub-populations that are separated geographically but connected by dispersal.

Individual habitat islands and their populations are often ephemeral. Yet the constant production of new habitat islands can lead to long-term survival of the species, depending on the balance between local extinctions and recolonizations in the patchwork of fragmented landscape (Hanski, 1999). The process permits "the metapopulation persistence of unstable but more or less independently fluctuating local populations" (Hanski, 1999, p. 11).

This model provides a good description of the population dynamics in many species that inhabit active volcanic archipelagos. Metapopulations persist there through constant colonization of younger, active islands from older, extinct ones, and the latter eventually subside. Volcanic islands are short-lived in geological time, but the volcanic centres that generate them are much older. Most archipelagos in the central Pacific, for example, have been active for tens of millions of years, although their current islands are all much younger than this

The metapopulation model explains how a group can *survive* in a dynamic region. In addition, active volcanic centres are often rifted apart into separate, active sections (e.g. at subduction zones offset by transform faults), and so it is likely that the populations there can also *differentiate*. If an active volcanic archipelago hosting a metapopulation is divided into separate, active segments moving away from each other, the genetic cohesion of the metapopulation will be reduced and eventually fail, and vicariance into two or more metapopulations can result. Thus, tectonic changes, including those discussed below, can break up widespread insular metapopulations and produce endemics restricted to fewer islands or even a single island. Many regional zones of oceanic volcanism have been rifted apart, and so clades endemic to young volcanic islands there are likely to originate by vicariance of widespread ancestors. For example, a group inhabiting young volcanic islands in western Polynesia and its sister group with similar ecology in eastern Polynesia could both be derived from a widespread Pacific group that has been ruptured by sea floor spreading at the East Pacific Rise. Molecular phylogenetic studies are documenting a growing number of such patterns, with precise allopatry among terrestrial, insular clades that each occupy a large sector of the Pacific (Heads, 2012, 2014), and these could be the result of simple vicariance in an oceanic setting.

This "metapopulation vicariance" model of island biogeography differs from the standard one in the significance attached to former islands. In traditional theory, these act as "halting-places" or "stepping stones" that facilitate migration of rare individuals from a continent to a distant island. In contrast, the metapopulation model proposes that the sequential emergence of past, present and future islands allows a metapopulation to survive in its particular region, more or less *in situ*, and so it is not necessary to assume that the groups have dispersed there from a continent. In theory, a lineage can persist in an insular region more or less indefinitely, for as long as new islands are being produced.

Earlier theories of island biogeography

The "equilibrium theory of island biogeography"

Island biogeography has been explained in several ways. The best known is MacArthur and Wilson's (1967) "equilibrium theory of island biogeography". This proposed that the two main processes determining an island's biota were *dispersal* from the nearest mainland, and *extinction* of groups on the island. Variation in these processes was in turn attributed to the island's area and its distance from the mainland. The theory did not consider the island's specific *location* on the Earth's surface, or the *tectonic history* of the volcanic centre that produced the island.

MacArthur and Wilson's (1967) model is still widely accepted. For example, one illustrated scenario for a new volcanic island began with a large blank space labelled "Nothing" (Gillespie and Roderick, 2002, fig. 1). In this scenario, the site has no geographical location and, in particular, no tectonic context.

Although MacArthur and Wilson (1967) assumed that mainland-to-island dispersal is a key factor determining island biota, "migration among the islands is ignored" (Hanski, 2010, p. 189). Yet migration among neighbouring islands is a common process, and it is probably critical for evolution. This is not because it leads to speciation, but because it allows the persistence of metapopulations more or less *in situ*, for example, in the region occupied by a single archipelago.

The "general dynamic model (GDM) of oceanic island biogeography"

A recent model of oceanic island biogeography represents an advance over the ecological approach of MacArthur and Wilson (1967), as it incorporates the geological "life cycle" of a volcanic island, from small to large and then small again (Whittaker et al., 2008, 2010). "The general dynamic model of oceanic island biogeography (GDM) has added a new dimension to theoretical island biogeography in recognizing that *geological processes* are key drivers of the evolutionary processes of diversification and extinction within

remote islands." (Borregaard et al., 2017, p. 830; italics added). This general approach is advocated here. Studies in comparative biogeography have often integrated geological and biological data, for example, in analyses of old taxa endemic on young islands (Heads, 2011).

A detailed review of the GDM by Borregaard et al. (2017) only mentioned metapopulations once: "connectivity serves to reduce extinction rates by facilitating metapopulation dynamics" (p. 839). But connectivity implies other processes in addition to simple survival; for example, what happens if the connectivity in an active archipelago changes? The GDM is not yet general or dynamic enough to answer this question; it does not incorporate the tectonic changes that can take place in an active archipelago, and so it overlooks the metapopulation vicariance that this is likely to cause. Although it represents an advance over the equilibrium theory of island biogeography, the GDM still only considers geological evolution at the spatial and chronological scale of an individual island: "The critical parameter for establishing the timescales of biological evolution on oceanic islands is the age of emergence of an island … " (Triantis et al., 2016, p. 2). In fact, however, as Triantis et al. (2016, p. 3) also wrote, "the current geography of the archipelago may be misleading of the configuration(s) relevant to understanding the evolutionary assemblage processes … most archipelagos are older than the oldest extant island … ". This important principle of dynamic tectonic development also explains the fact that many island endemics are much older than their current island (Heads, 2011).

Borregaard et al. (2017) supported the notion that "the spatial arrangement of islands within an archipelago and *how this changes over time* may have an important influence on gene flow and differentiation within archipelagos …" (p. 3; italics added). Yet in their section on "archipelago dynamics", they referred only to the rise and subsidence of individual islands, to whether or not islands have ever been conjoined, and to Pleistocene sea level change. In fact, volcanic archipelagos can undergo a wide range of tectonic changes; these include subsidence with sea floor cooling and with volcanic loading, and rifting of subduction zones and intraplate volcanic centres at transform faults and spreading ridges.

Geology of oceanic islands

A small number of oceanic islands, such as Macquarie Island south of New Zealand, are tectonic in origin and represent upfaulted sea floor, but most oceanic islands are formed by volcanism. Volcanic islands do not develop at random sites, but at volcanic centres of different kinds. These occur along active plate margins, where volcanism might be expected, but they are also found far from plate margins at intraplate localities. Both kinds of centres usually produce multiple islands over long periods of time, and they are older than the individual islands.

Plate margin volcanism

Volcanic arcs along subduction zones can occur in continental crust, for example along the Andes, or in oceanic crust, for example in the Lesser Antilles and Melanesia. Andesite (named after the Andes) is a typical feature of subduction zones and the volcanic arcs that they produce, whether in continental or oceanic settings. In intraplate settings, volcanic islands often form linear chains and are instead composed of alkali basalts (oceanic island basalt). Normal sea floor crust produced at mid-ocean spreading ridges (and also terrestrial flood basalt) is tholeiitic basalt.

Intraplate volcanism

The causes of intraplate volcanism are the subject of current debate (Foulger et al., 2013). In the traditional model, intraplate volcanism develops above a hot, narrow, deep mantle plume, but the tomographic evidence can be interpreted in different ways. Also, some lines of intraplate volcanics, such as the Cameroon Volcanic Line, do not show a simple linear sequence in the ages of the individual volcanoes. In some regions, such as the eastern South Island, New Zealand, volcanism has persisted in the same area for long periods, even though the plate has moved and the South Island would have moved away from a mantle plume hotspot. French Polynesia contains five major volcanic chains, with each attributed, "sometimes with great difficulty", to the drift of the Pacific plate over hotspots (Bonneville, 2009, p. 339). The chain in the Marquesas Islands deviates 20–30° from the direction of the absolute plate motion, and this deviation is "quite odd" (Bonneville, 2009, p. 342). The Cook–Austral island chain has age distributions that are "particularly difficult to resolve based on the hotspot hypothesis … [there is] a wide geographic range of recent [and older] volcanism" (Rose and Koppers, 2014, p. 1).

To deal with these problems, some geologists have suggested complex, *ad hoc* hypotheses, such as multiple hotspots in an area, hotspots that turn on and off, and hotspots that move. Other geologists have rejected mantle plumes in the traditional sense as a cause of intraplate volcanism, and instead they have proposed mechanisms based on plate tectonics effects in the crust (Smith, 2007; Anderson, 2010; Hamilton, 2011). Propagating fissures in the crust caused by flexing and extension, rather than mantle plumes, could explain lines of volcanism in which the individual volcanoes

along the line follow a simple age sequence, and also lines of volcanism without an age sequence.

Metapopulations and volcanism

Outside a few specific localities, notably Hawaii, the concept of metapopulations is seldom related to oceanic island volcanism. Standard texts on metapopulations (e.g. Gilpin and Hanski, 1997; Hanski, 1999, 2010; Hanski and Gaggiotti, 2004) make little reference to volcanism. In one leading textbook on island biogeography, the section on metapopulations (in Chapter 10) does not mention volcanism, while the section on volcanism (in Chapter 2) does not mention metapopulations (Whittaker and Fernández-Palacios, 2007).

This neglect is probably because the usual concept of metapopulations, as adopted by many authors, spans only ecological timescales; in metapopulations: "the timescale of their dynamics ... may be of the order of decades" (Whittaker and Fernández-Palacios, 2007, p. 263). However, metapopulations also have a biogeographical and geological context, and they may persist for tens of millions of years. For example, in molecular clock studies the frog *Leiopelma hochstetteri*, endemic to the New Zealand archipelago, has been dated as Cretaceous (67 Ma; Carr et al., 2015).

Molecular evidence for metapopulation dynamics: old taxa endemic to young volcanic islands and mountains

Groups that exist as endemic metapopulations at volcanic centres can be much older than the individual islands themselves. This principle has become more widely accepted following the publication of molecular clock dates. Fossil-calibrated clock dates give minimum clade ages, and these show that many clades are older than the islands they are endemic to (Heads, 2011). The results suggest that a young island could have been populated by endemics from nearby, older islands that later sank below sea level, leaving the groups endemic to the young island. As long as new volcanic islands are being produced, the plants and animals in the region can survive by a process of perpetual hopscotch.

Some young islands with endemics dated as older were listed earlier (Heads, 2011), and additional cases are constantly being reported. For example, a clade of Malvaceae ("Clade A") endemic to Mauritius and Réunion in the Mascarenes was dated as much older than the current islands (Le Péchon et al., 2015). The authors wrote that "Traditional interpretations of insular radiations often assume that endemic taxa radiated after the origin of the insular habitats on which they were established ... " (p. 211). In contrast, the authors concluded: "The clade A pattern of old taxa on young islands indicates diversification before the formation of the Mascarenes, and this characteristic *is inconsistent with traditional scenarios of insular diversification ... "* (p. 218; italics added). The origin of clade A was probably related to prior tectonic events that affected former islands in the Mascarenes region (Ashwal et al., 2017).

Extinction on subsiding islands

Metapopulations of terrestrial organisms can survive in a zone of oceanic island volcanism for as long as this is active. If the centre becomes inactive, the populations there will go extinct, one by one, as the islands erode and subside and no new ones are formed. Biological evidence for this sort of extinction includes fossil material of high island organisms, such as wet-forest landsnails, on what are now low, sparsely vegetated atolls—former high islands—in the Pacific (Heads, 2012, p. 280). A small number of organisms can survive the harsh atoll environment, and these will persist in the region for much longer.

Metapopulation survival in oceanic island systems

Metapopulation survival on single volcanic edifices

De novo volcanic edifices occur as islands in the ocean basins and, as habitat islands, in continental settings. As Darwin (1859, p. 380) observed, "A mountain is an island on the land". Belts of volcanism on continents include arcs (as in the Andes) and rift zones (as in the East African "arc" mountains). Endemics on the volcanoes include species that are dated as older than the individual volcano they inhabit; an example is the cricket *Monticolaria kilimandjarica* endemic on Kilimanjaro, by the Great Rift Valley (Heads, 2012, p. 71). One explanation is that communities have survived more or less *in situ* by small-scale metapopulation dynamics, as the separate eruptions do not cover the whole mountain at any one time. New lava and ash is colonized, as soon as it cools, by organisms from neighbouring areas of older strata. Later, the colonized areas can act, in turn, as sources for colonization of other, newer deposits in the vicinity.

Metapopulation survival at an intraplate volcanic centre: the Hawaiian Islands

The most-discussed case of intraplate island biogeography is the Hawaiian archipelago. One theory accepts that the Hawaiian biota has survived as metapopulations; the islands are thought to have formed continuously as the plate moved over a mantle

plume, and successive new islands have been colonized by populations from older ones (Beverley and Wilson, 1985). In the Hawaiian chain, the oldest high island (Kauai) formed at ~5 Ma and the oldest emergent island (Kure atoll) at ~30 Ma, but the oldest submerged seamount that has been dated, Detroit Seamount near the north-western end of the chain, formed at 81 Ma (Cretaceous). This provides a minimum age for the chain; its actual age is unknown, as the rest of it has been subducted beneath Asia.

Triantis et al. (2016) accepted the metapopulation model for oceanic islands and wrote: "Within volcanic archipelagos comprising islands of multiple geologic stages, for the younger, growing islands, the nearby older islands are generally the dominant sources of colonizers … Species may be dynamically colonizing and going extinct from islands within an archipelago, but the species presence, i.e. *the metapopulation at the archipelago level, is conserved*". (p. 7; italics added).

Triantis et al. (2016) noted that the Hawaiian lobeliads (Campanulaceae) had an origin "13 million years ago (more than twice the age of the current oldest large island) … " (p. 5). The authors concluded: "understanding diversity dynamics at the island or even the archipelagic level, necessitates understanding of the dynamics at the *meta-archipelagic, regional* level … " (p. 6; italics added). This approach, adopted here, also stresses the *former* high archipelagos around Hawaii, such as the Musicians seamounts to the north, and the atolls of the Line Islands to the south.

Apart from the lobeliads, several other Hawaiian endemics have been dated as older than the present islands of the archipelago. These include the plants *Hillebrandia* (Begoniaceae, sister of *Begonia*), *Hesperomannia* (Asteraceae) and "*Peucedanum*" *sandwicense* (Apiaceae) (Heads, 2012; Spalik et al., 2014). Spalik et al. (2014) observed that the existence of these old lineages on a young island may be explained by their survival on former islands in the Hawaiian chain, or on other island groups in the region. They may also have occurred on *former* island groups in the region.

Dispersal theorists have occasionally considered dynamic, metapopulation-style survival on young volcanic islands, but they have rejected it. O'Grady et al. (2012, p. 703) wrote: "it is a fantastical conjecture to propose that single metapopulations have existed perpetually … ". No-one is suggesting they have existed for all time, but if volcanic centres are active for millions or tens of millions of years, as they often are, it is likely that metapopulations in the same region are just as old.

O'Grady et al. (2012, p. 703) wrote that: "metapopulation theory fails to explain how taxa may persist for millions of years on terrestrial real estate that has yet to exist. Geologically, most oceanic archipelagos have formed intermittently, with periodic lulls leaving large evolutionary time between emergences [of any islands]". The authors cited just one example as evidence for this idea; they wrote: "Our *well-supported understanding* of the geologic processes underlying [Hawaiian] island formation precludes the panbiogeographic persistence of metapopulations in any real sense." (p. 703; italics added). But this glosses over a key problem—calculating the heights of former islands.

Many biologists have accepted that in the Hawaiian region "there was a period between at least 33 and 29 Ma in which no islands existed, and distant colonization was thus crucial … " (Triantis et al., 2016, p. 5). Nevertheless, the heights of the former islands were estimated from the present surface area of the volcanoes, assuming a 7° slope for subaerial lavas (Clague, 1996; Price and Clague, 2002). There is a great potential for error in these calculations, and Clague (1996, p. 40) stressed that estimating the longevity of an island "is far more complex and, therefore, far more uncertain than estimating either the age or size of the volcanoes". Other authors have also noted that the results are "fairly approximate" (Whittaker and Fernández-Palacios, 2007, p. 30). In fact, the method considerably underestimates the heights of present volcanoes, and so it probably also underestimates the heights of past volcanoes (Table 1). Despite this, the idea that there were no emergent Hawaiian islands between 33 and 29 Ma is now well entrenched in the literature, and it forms the entire basis of the theory that all Hawaiian groups (and the biotas of all other similar archipelagos) dispersed there. Instead, it is likely that terrestrial groups have existed in the region since the origin of the chain, at some time before the origin of the oldest dated seamount, Detroit Seamount, in the Cretaceous (81 Ma).

O'Grady et al. (2012, p. 704) criticised the idea of "widespread connectivity across the paleo-Pacific via metapopulations inhabiting a series of Atlantean [i.e. mythical] archipelagos … because of lack of evidence for intervening populations and suitable island habitat in the region". Yet they overlooked the geological

Table 1

Actual heights of volcanoes on Maui and Hawaii, and maximum heights predicted by Clague (1996)

Volcano	Actual height (m)	Clague (1996) estimate of height (m)
E Maui	3055	2180
Kohala	1670	1740
Hualalai	2521	1040
M. Kea	4205	3050
M. Loa	4170	3050
Kilauea	1277	1040

evidence for prior land that was cited in the work they were criticising (Heads, 2012). Thousands of atolls and submerged, flat-topped seamounts (guyots) occur on subsided sea floor throughout the Pacific, and all these are former high islands. Maps of the ocean floor are far from complete, and only ~15 000 out of possibly ~200 000 seamounts more than 1 km in height have been mapped; there are better topographic maps of the Moon and Mars (Heads, 2012, p. 326). Thus it is not too surprising that in 2005 the nuclear submarine U.S.S. *San Francisco* was involved in a fatal collision with an uncharted seamount, south of Guam.

In addition to the evidence for islands on unthickened sea floor, there is also good evidence for sub-aerial eruptions on the large igneous plateaus of the central Pacific, and the volcanics include fossil wood in intercalated sedimentary strata.

Metapopulation survival along active plate margins

Volcanism along a subduction zone will generate new habitat and allow metapopulation survival for as long as subduction continues (Fig. 1). Many clades are endemic to these zones and survive there as "volcano-weeds". An example is the shrub *Scaevola gracilis* (Goodeniaceae), restricted to the Kermadec and Tonga Islands north of New Zealand. The active Kermadec–Tonga Ridge lies over the Australia plate/Pacific plate boundary. In Tonga, Eocene volcanics are exposed on 'Eua, but *S. gracilis* is only known from younger islands, including Tofua in Tonga and Raoul Island in the Kermadecs which are still active. *S. gracilis* is most common on Raoul Island, where it forms dense stands on open pumice slopes in the main crater (Sykes, 1998).
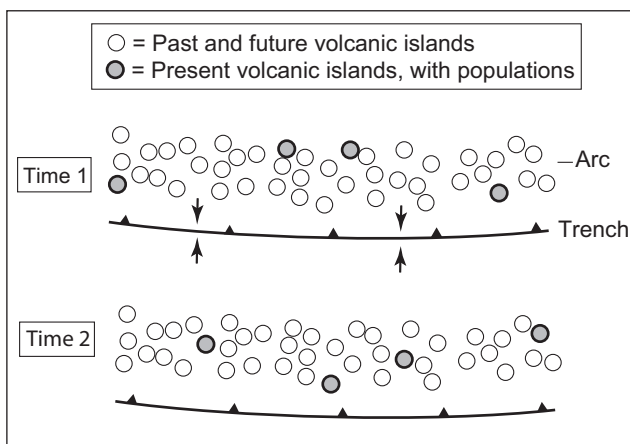

Fig. 1. Survival of a metapopulation along the island arc of an active subduction zone. The barbed line indicates the trench, with the barbs on the over-riding plate. Arrows indicate plate movement. Volcanic arcs are located along subduction zones on the over-riding plate, ~200 km back from the trench.

The volcano-weed *Scaevola gracilis* appears to be well adapted to life on a subduction zone and, within its sector of the margin, has probably been colonizing new volcanoes as they appeared for millions of years, much longer than the age of any individual island. Raoul Island endemics include many species and even genera, including the terrestrial isopod genus *Okeaninoscia* (Schmalfuss, 2003).

Island formation along the Kermadec–Tonga arc is ongoing. In 2015, volcanic eruptions in Tonga created a new island 1.7 km across and 100 m high between the islands of Hunga Tonga and Hunga Ha'apai. The island was composed of ash and large rock fragments, and the first visitors reported that "There are thousands of seabirds—all kinds, laying eggs on the island" (*Telegraph,* 2015).

Physical contact between islands is not necessary for metapopulation vicariance

It is usually assumed that vicariance of terrestrial groups can only take place in a continuous population on an area of continuous land. Thus, because most volcanic islands have never been joined with any other land, it is inferred that their terrestrial endemics must have been derived by dispersal.

Gillespie and Roderick (2002) wrote that for island systems, the primary distinction is between "fragment" islands that were joined to other land in the past, and "darwinian" islands that formed *de novo*; the latter "have never been *in contact* with the source of colonists" (p. 595; italics added). This emphasis that biogeographers have placed on physical contact has obscured the importance of metapopulations that inhabit unconnected islands.

Whittaker and Fernández-Palacios (2007, p. 19) proposed that a vicariance origin for an island biota requires "the breaking of a past land connection". The authors accepted vicariance as a possible mode of evolution on continental fragment islands, such as Madagascar, but "For true oceanic islands, the starting point is different: dispersal across a pre-existing barrier" (Whittaker and Fernández-Palacios, 2007, p. 203). *In situ* speciation by vicariance is thus accepted for differentiation within single islands and archipelagos, but it is ruled out for large oceanic regions, such as west Pacific islands vs. east Pacific islands, or east Pacific islands vs. America.

The suggestion that vicariance can only take place within a single, completely continuous population is a popular one, but it appears to be flawed. Most species, and presumably most ancestors, have patchy distributions, with separate populations connected by normal, ecological dispersal. This dispersal occurs, for example, between populations located in different parts of one

island, and among populations on different, neighbouring islands. The process is not long-distance dispersal in the sense of biogeographers, as: (i) it is observed, not inferred; (ii) it involves the regular, repeated movement of many individuals or diaspores, not events that are rare or unique in geological time; and (iii) it does not lead to speciation or indeed any differentiation. This "normal" dispersal—unlike long-distance dispersal—is a key process that needs to be incorporated in analysis, not because it causes speciation (it does not), but because it enables metapopulation survival in a dynamic environment.

All individual organisms that establish anywhere have dispersed from their point of origin, across areas of land or water, and if there are available sites the metapopulation will survive. Whether the sites are connected by continuous land is irrelevant to the basic population dynamics; propagules of a species may cross a fence or a stream, an area of land or a seaway, as a regular part of the species' ecology. A metapopulation surviving in this way, especially a widespread one, is likely to be polymorphic, but if conditions remain constant it will not differentiate into distinct new species.

O'Grady et al. (2012) criticised the idea of metapopulation vicariance in the central Pacific (Heads, 2012), writing that it "really is not a theory at all" because "the lack of any significant connections between these remote islands and the mainland, are ignored" (p. 703). But this lack of connection is not ignored; instead, it is the whole point of the metapopulation concept—the subpopulations are not connected by continuous, suitable habitat, but they are connected by dispersal and gene flow.

In rejecting the "panbiogeographic persistence of metapopulations" and its relevance for island biogeography, dispersal theorists (O'Grady et al., 2012, p. 703) reject the normal, overwater dispersal that is often observed taking place over, say, tens of kilometres within archipelagos. Yet, at the same time, dispersal theory accepts that the biota of remote island groups such as Hawaii is derived entirely by long-distance dispersal over thousands of kilometres. The position seems untenable.

Metapopulation vicariance in oceanic island systems: tectonic mechanisms

Geological change in systems of oceanic islands

As Borregaard et al. (2017, p. 836) wrote: " … the spatial arrangement of islands within an archipelago and how this *changes over time* may have an important influence on gene flow and differentiation within archipelagos". (italics added). How exactly do changes in the spatial arrangement of oceanic islands and archipelagos take place?

Pleistocene sea level change is one obvious mechanism, and it is the only mode of vicariance among islands that is accepted in dispersal theory. For example, for many years it was the usual explanation for clade distributions in the Philippines. Yet most molecular studies of Philippines groups now agree that the model is flawed. This is because there is no spatial agreement between the main patterns of clade distributions and the geography of the Pleistocene islands, and because the minimum clade ages calculated in clock studies are older than the Pleistocene (Heads, 2014, chapter 10). The new molecular evidence suggests that the events in Earth history that are relevant for evolution in the Philippines were tectonic in origin and pre-Pleistocene in age.

In oceanic environments, vicariance of terrestrial and reef metapopulations would be expected to accompany particular types of tectonic change in the crust that are well documented at plate margins and intraplate volcanic centres. The next sections deal with some of these processes.

Vicariance caused by volcanic loading and subsidence

The growth of oceanic islands by repeated eruptions is often followed by subsidence of the edifices caused by the weight of the rocks—volcanic loading—and isostasy. These processes "have reiteratively mixed and isolated populations, creating a mechanism for vicariant speciation" (Triantis et al., 2016, p. 3). The Hawaiian Islands provide good examples of vicariance probably caused by subsidence, and the process is often accepted for islands in the group that were once joined. Borregaard et al. (2017, p. 836) stressed that: "O'ahu was in the past briefly *conjoined* to Moloka'i, which then became conjoined with Lana'i, Maui, and Kaho'olawe to form Maui Nui … , although they are currently *separate* islands" (italics added).

However, as stressed already, islands do not have to be *conjoined* and then separated for metapopulation vicariance to occur. If islands that were never connected are close enough for normal dispersal to occur between them, ancestral forms can exist as metapopulations. If the distance between the islands then *increases* with subsidence, vicariance can develop between the islands. The former metapopulation can then evolve into endemics restricted to fewer islands or to single islands.

For example, several groups in the Hawaiian archipelago display a break between a clade on Hawaii island and its sister-group on the other islands (review in Heads, 2012, p. 366). Hawaii and its nearest neighbour, Maui, were originally 8 km apart, but following volcanic loading they are now 50 km apart. Organisms

that can disperse 8 km and maintain a metapopulation are not necessarily able to disperse 50 km, and so for many groups vicariance would result. This mode of speciation does not seem to have been discussed for Hawaiian taxa.

Vicariance caused by sea floor cooling and subsidence

As sea floor drifts away from the spreading ridge that is producing it, it cools (increasing its density) over tens of millions of years, and subsides by large amounts (van der Pluijm and Marshak, 2004). This leads to the submergence of many islands that had developed on it earlier; most current high islands on older oceanic crust, such as the Hawaiian group, are new ones. Modern dispersal models for oceanic islands either do not acknowledge this massive subsidence (e.g. Cantley et al., 2016) or even reject it (O'Grady et al., 2012), but it is another likely cause of breaks in metapopulations on groups of oceanic islands.

One recent analysis of the Hawaiian Islands biota stressed the former islands in the central Pacific that are now submerged, and it mapped the 2000-, 4000- and 5000-m isobaths in the region (Heads, 2012, figs. 7-1, 7-2). Yet Holland (2012, p. 146) wrote that "the figures appear to be a disingenuous and misleading depiction aimed at advancing the vicariant agenda". O'Grady et al. (2012, p. 704) agreed that the figures were "more than slightly disingenuous", as sea level has not dropped by more than ~100 m, and so the many submerged seamounts could not have been emergent. Nevertheless, all these authors overlooked the *thousands* of metres of subsidence that the Pacific sea floor itself has undergone through the Cenozoic (van der Pluijm and Marshak, 2004, p. 404; Hillier and Watts, 2005; Zhong et al., 2007, fig. 1).

Vicariance caused by migration of an arc away from a continent

Biogeographers are well aware that the two plates converging at an active subduction zone are mobile, but they often neglect the fact that subduction zones themselves, along with their associated arcs, can also move. Usually the trench marking the subduction zone retreats towards the subducting plate. The process takes place by slab rollback, with the descending slab of crust falling backwards even though its plate is moving forwards, as in a retreating wave on a seashore.

Slab rollback can lead, for example, to the migration of a volcanic arc away from the edge of a continent and far into the ocean. This is another way in which a metapopulation can be subdivided (Fig. 2). There is no fundamental difference between a metapopulation on a drifting island arc and one on a drifting continent. In both cases the organisms survive by dispersal among suitable habitat patches, whether these are new islands in an arc or, for example, new mountains on a continent.

Slab rollback is thought to be a fundamental process in the development of the south-west Pacific (Fig. 3). The history there over the last 200 Myr has been dominated by the following processes:

1. Accretion of oceanic terranes (including seamounts and island arcs) from the pre-Pacific onto continental crust, with associated uplift.

2. Pre-drift rifting and magmatism (from ~100 Ma to 80 Ma).

3. Gondwana breakup with sea-floor spreading.

4. Migration of the main Pacific subduction zone and its island arc by slab rollback into the Pacific (~90 Ma onwards). So far, the subduction zone has migrated as far east as Tonga–Kermadec Islands–New Zealand. As the arc migrated eastward, a series of backarc basins, including the Tasman and Coral Sea basins, opened behind it. (Backarc basins are localized, divergent rifts, but are formed in zones of overall plate *convergence*.) Some of the basins opened in the continental crust of Gondwana and caused its breakup (Fig. 3). Some of the backarc basins, notably the South Loyalty basin, opened but then later closed.

5. Development and migration of other subduction zones behind the first belt (Fig. 3).

These processes all led to profound geographical changes that are likely to have caused vicariance, for example in widespread Pacific and Indo-Pacific ancestors.

The neglect of slab rollback in biological work has led to problems in dating studies. For example, a study of Fijian taxa calibrated a phylogeny using a suggested age of Kadavu Island in southern Fiji (1.5–2.5 Ma) to date endemics there (Monaghan et al., 2006). The geological age was based on the age of exposed volcanic strata on the island. These strata belong to the current phase of volcanism, in which ocean island basalts (typical of intraplate volcanism) have been erupted and emplaced over earlier rocks.

Nevertheless, before the latest volcanism, a prior arc passed through Fiji (the extinct trench "1" in Fig. 3) and instead produced andesites, typical of subduction zones. Exposed rocks of this earlier phase are dated from the Eocene to Miocene (Colley and Hindle, 1984; Cronin et al., 2003).

Yet the history of volcanism in the antecedents of the Fijian archipelago probably goes back even further. Regional tectonic models propose that the subduction zone and its island arc date back to the Cretaceous, when the ancestral arc migrated away from the proto-Australian part of Gondwana (Fig. 3). This slab rollback and the long history of earlier islands is probably
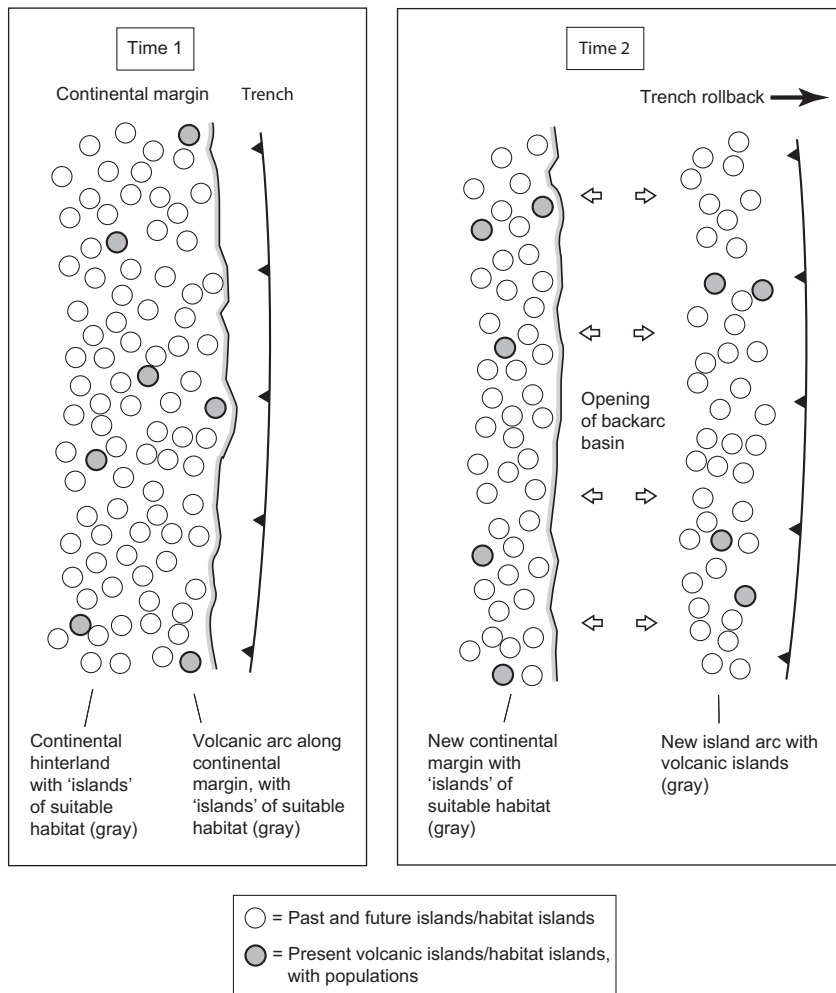
Fig. 2. Migration of a subduction zone and its arc away from a continent by slab rollback.

more important for the biogeographical history of Fiji than the age of the current islands.

The SW Pacific sea floor includes many ridges with distinctive, linear morphology. These can represent ribbons of continental crust (Norfolk Ridge, Lord Howe Rise in Fig. 3), arcs at subduction zones (Loyalty–Three Kings, Lau–Colville, Tonga–Kermadec in Fig. 3), or mid-ocean spreading ridges (none are shown in Fig. 3).

Vicariance caused by the lengthwise splitting of an active subduction zone, with one active arc separating from another

One tectonic model for the Tasman–Coral Sea region proposes three sets of subduction zones (Fig. 3, simplified from Schellart et al., 2006). As the primary subduction zone migrated eastward into the Pacific, secondary and tertiary arcs developed behind it. The secondary subduction zones differed from the first in their subduction polarity, and they underwent *westward* rollback.

In one example of this, from 50 to 25 Ma the Loyalty Islands–Three Kings subduction zone and its arc (labelled "2" in Fig. 3) split off from the initial Pacific subduction zone (labelled "1" in Fig. 3). (Note that an arc is typically located ~200 km behind its associated trench.) Westward rollback of the new arc pulled the Loyalty Islands ridge (now part of the New Caledonia archipelago) away from proto-Vanuatu, until eventually it collided with the continental crust of mainland New Caledonia and Norfolk Ridge. At this point, subduction at the trench and volcanism along the arc both ceased.

This tectonic history would explain the great biological difference between the Loyalty Islands and the nearby mainland of New Caledonia, which is otherwise enigmatic. It would also explain the great similarity of the Loyalty Islands with the more distant Vanuatu (Heads, 2008). As the new, Loyalty arc formed, it would have been colonized from the adjacent primary Pacific arc, but with continued slab rollback the biotas of the two arcs have diverged.
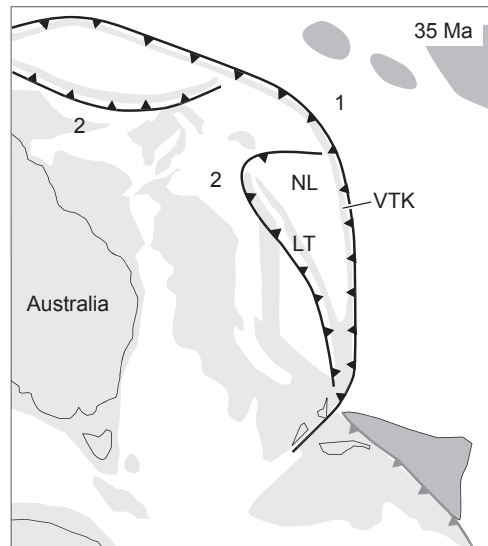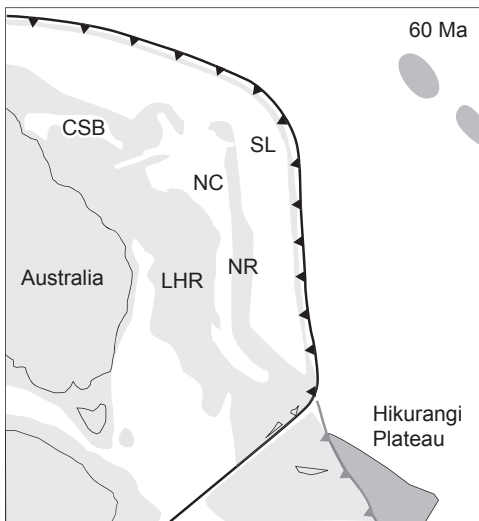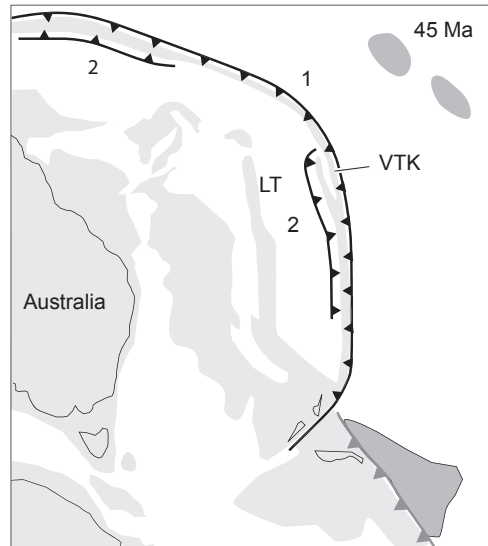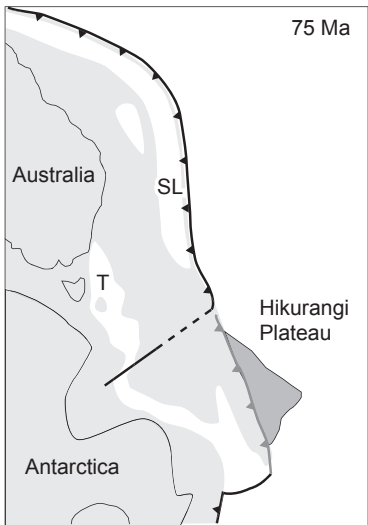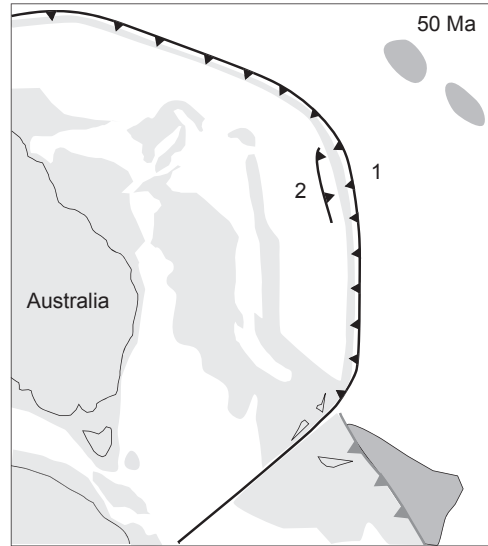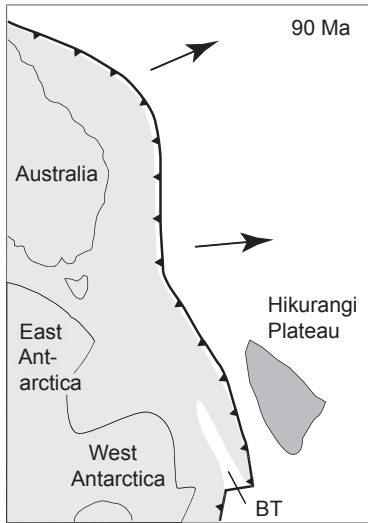
Fig. 3. Tectonic reconstruction of the south-west Pacific, from the Late Cretaceous to the Present. The reference frame is Australia-fixed. Light grey = continental crust and island arc crust; dark grey = oceanic plateaus. Geographical outlines are shown to help identify the location of the crustal blocks but have no palaeogeographical significance. Arrows in the 90-Ma reconstruction = migration of subduction zone by slab rollback. 1, 2, 3 = 1st, 2nd and 3rd generation subduction zones. BT, Bounty Trough; CSB, Coral Sea Basin; LC, Lau–Colville Ridge; LHR, Lord Howe Rise; LT, Loyalty–Three Kings Ridge; NC, New Caledonia Basin; NL, North Loyalty Basin; NR, Norfolk Ridge; SL, South Loyalty Basin; T, Tasman Basin; TK, Tonga–Kermadec Ridge; NF, North Fiji Basin; VTK, Vitiaz–Tonga–Kermadec Ridge. Simplified from Schellart et al. (2006).

Vicariance caused by the lengthwise splitting of an active subduction zone, with an active frontal arc separating from a remnant arc

The opening of a backarc basin behind a migrating oceanic arc can separate one active island arc from another, in which subduction and volcanism cease. For example, at ~15–10 Ma, the Ontong Java Plateau and the Melanesian Border Plateau arrived from the Pacific at the Vitiaz trench section of the Pacific plate subduction zone. These are large igneous plateaus, and their arrival blocked subduction along the Vitiaz trench; subduction then developed (with opposite polarity) along the trench at Vanuatu (labelled "3" in Fig. 3). The new trench propagated from the Bismarck Archipelago to the Solomon Islands, Vanuatu and Fiji.

In this case the Vanuatu–Fiji section of the primary arc (at the Vitiaz trench) has been left inactive. The
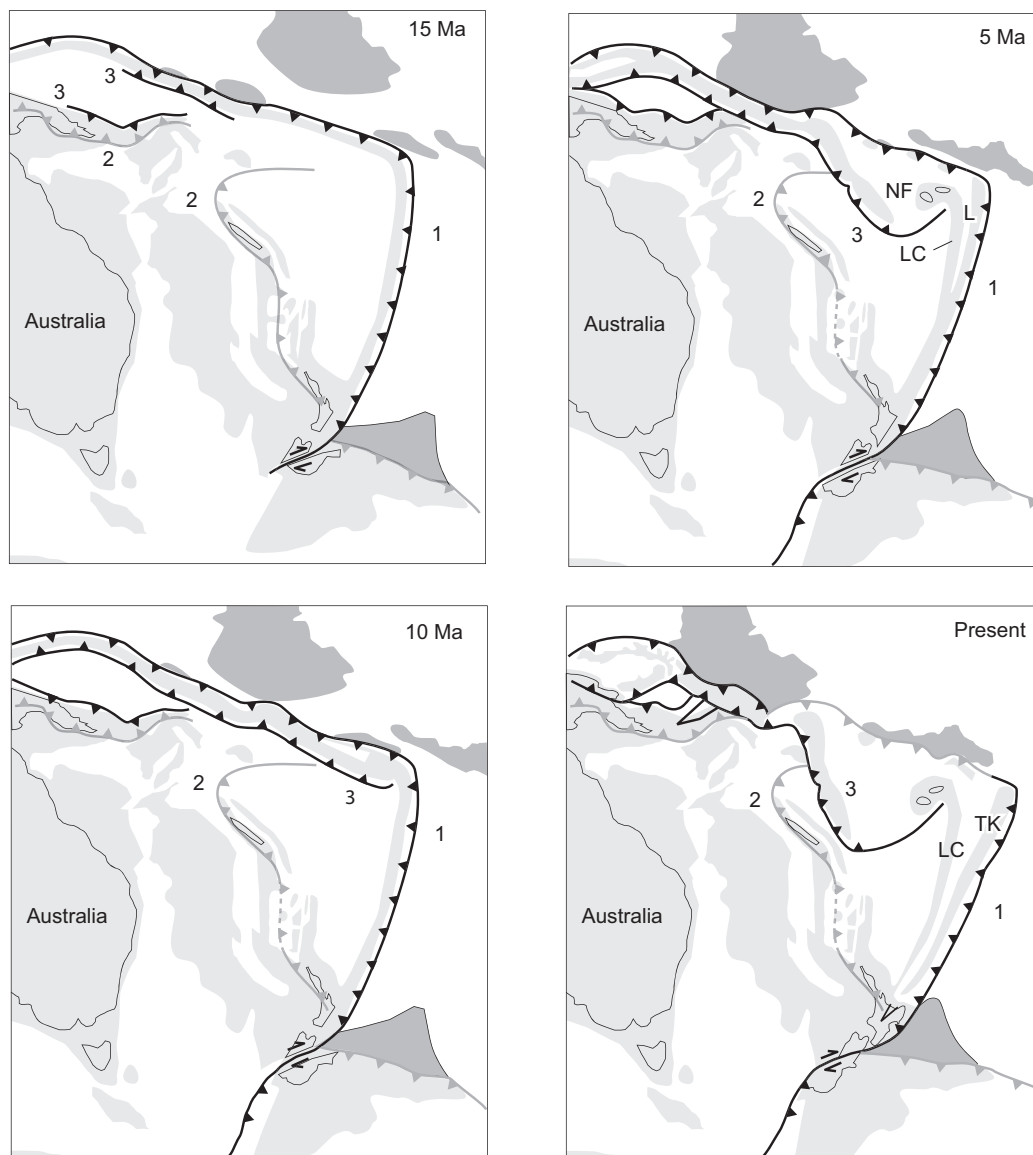

Fig. 3. Continued

new arc ("3" in Fig. 3) has probably inherited most of its biota from the old one.

Another case concerns the Lau group of islands in eastern Fiji (Fig. 3, reconstruction for 5 Ma). The Lau Ridge is a remnant arc that has subsided, but it is still emergent in parts and maintains a distinctive biota. This is known for its altitudinal anomalies, including otherwise montane species found near sea level on the subsided islands (Heads, 2006).

The Lau Ridge dates as a separate feature to 6 Ma, when the Tonga–Kermadec arc ("TK" in Fig. 3) on the oceanic side began to separate from the Lau–Colville arc ("LC" in Fig. 3) on the continental side and migrate eastwards away from it. The Lau–Colville arc then ceased activity. Ever since the separation of the Tonga arc, a backarc basin (Lau Basin) has been

rapidly opening between it and the Lau ridge, separating the biotas of Tonga and the Lau group. At the same time, the Fiji plateau has rotated anticlockwise to meet the Lau ridge (Martin, 2013).

The close biogeographical connections that the Lau group has with Tonga (rather than with western Fiji) are well known. For example, the landsnail *Samoana* and the parrot *Vini* each have species on Lau, Tonga and islands further east, but do not occur west of Lau, in the main Fijian islands (Heads, 2012, fig. 6-2 and 6-11). This pattern is consistent with the tectonic deformation that has taken place.

Vicariance caused by the fracturing and offset of subduction zones at transform margins

Geologists classify plate boundaries into three main kinds:

1. Convergent margins. These are marked by subduction zones and are usually associated with volcanism and uplift. Most plate margin islands are produced at subduction zones.

2. Divergent margins. These are marked by spreading centres, which may be either mid-ocean ridges or continental rifts.

3. Transform margins ("transforms"). These are marked by transform faults that display neither convergence nor divergence, but connect convergent and divergent margins (Fig. 4).

Transform faults are strike-slip faults in which the plates slide past each other horizontally rather than vertically. Unlike most strike-slip faults, transform faults cut through the entire lithosphere and thus act as plate margins. Transforms connecting two
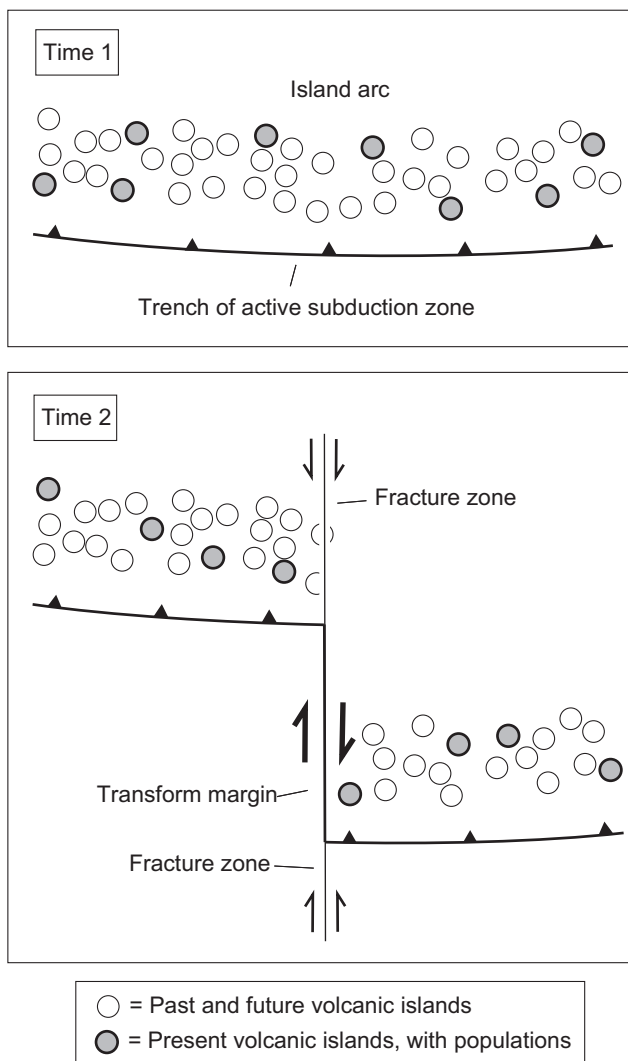

Fig. 4. Disjunction at a subduction zone (barbs on over-riding plate) caused by strike-slip displacement at a transform margin. Note the lack of current strike-slip on the fracture zones and the lack of volcanism along the transform.
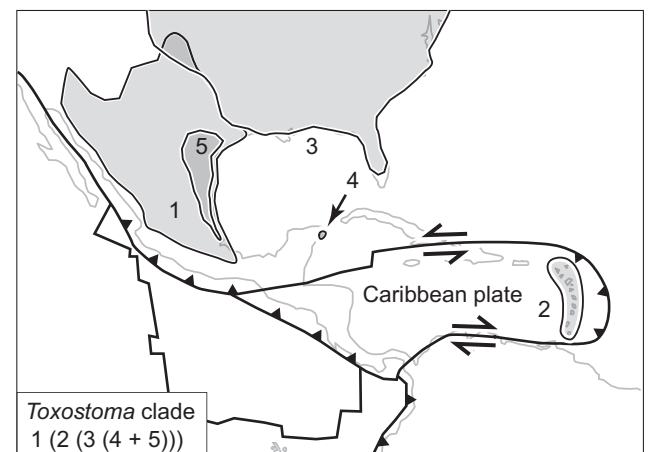

Fig. 5. Distribution of a clade in *Toxostoma* (Mimidae). 1 = *T. curvirostre*, 2 = *T. ocellatum*, 3 = *T. rufum*, 4 = *T. guttatum*, 5 = *T. longirostre*. Phylogeny from Lovette et al. (2012); distributions from IUCN (2016). Continuous lines = divergent and transform plate margins. Lines with barbs = subduction zones (barbs on over-riding plate). Plate boundaries simplified.
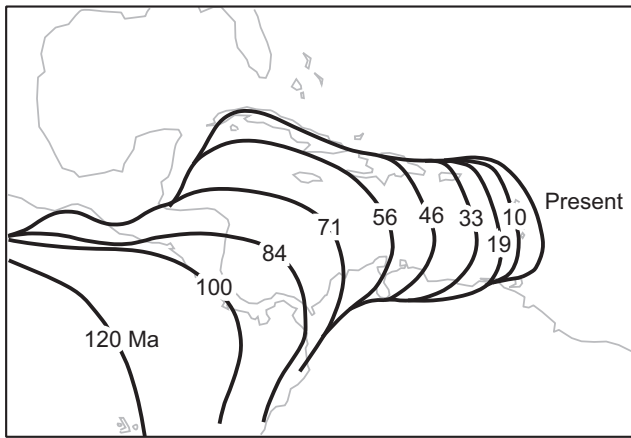
Fig. 6. Former relative positions of the Caribbean Trench from 120 Ma to the Present. The base map has no palaeogeographical significance; over the time period shown, North and South America have drifted apart (Pindell and Kennan, 2009).

subduction zones can cut though continental crust (as at the Alpine fault in New Zealand, the San Andreas fault in California and the southern margin of the

Caribbean plate), or through oceanic crust (as at the northern margin of the Caribbean plate).

Active transform margins continue beyond their junction with a convergent or divergent margin as faults termed fracture zones (Fig. 4). There is no current strike-slip displacement on the fracture zones, as the crustal blocks on each side (both part of the same plate) are moving at the same speed and in the same direction. Active strike-slip is restricted to the transform. (Fracture zones display evidence of *past* strike-slip, however, as the crustal blocks on opposite sides of a fracture zone have different ages).

Island arcs along convergent plate margins have often been offset by displacement at transform faults. At the time of the displacement, metapopulations on the island arc segments will also have been rifted apart, and this would generate vicariance and endemism along the plate margin. This provides a simple explanation for the 2600-km disjunction in the bird *Toxostoma* (Mimidae), between Mexico (Cozumel Island) and the Lesser Antilles (Fig. 5). The gap in the range can be explained by the displacement that has occurred along the northern and southern margins of
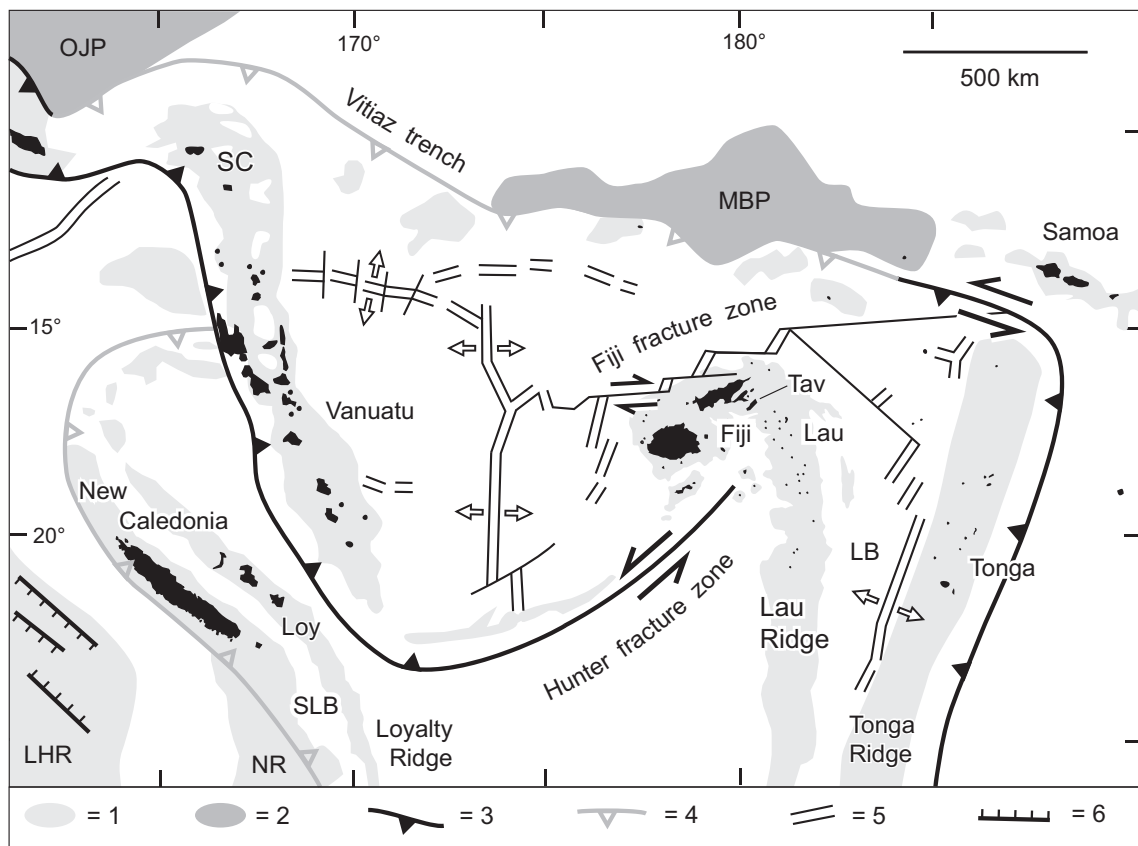

Fig. 7. Tectonics of eastern Melanesia (after Schellart et al., 2006; Martin, 2013). 1 = Continental crust (LHR and NR) and arc crust; 2 = Oceanic plateau; 3 = Active subduction zone (barbs on over-riding plate); 4 = Extinct subduction zone; 5 = Mid-ocean spreading ridge; 6 = Normal (extensional) fault; LB, Lau Basin; LHR, Lord Howe Rise; Loy, Loyalty Islands; MBP, Melanesian Border Plateau; NR, Norfolk Ridge; OJP, Ontong Java Plateau; SC, Santa Cruz Islands; SLB, South Loyalty Basin; Tav, Taveuni.

the Caribbean plate (Fig. 6), and passive transport of the bird populations. The strike-slip has accommodated the eastward migration of the active Caribbean trench with its arc; the zone of volcanism has rolled back through mainland America to its present position in the Lesser Antilles, where it remains active.

In the SW Pacific there has been a complex history of subduction zone development over the last 100 Myr, and the belts are offset in many places by transforms. The island arc archipelagos of Vanuatu and Fiji provide a good example (Fig. 7). The two together form an important centre of endemism that is well defined by about 20 seed plant species or putative sister species (23 if the Santa Cruz Islands are included with Vanuatu) (Smith, 1979–1996). For example, the palm *Neoveitchia* comprises one species in Vanuatu and one in Fiji, while *Balanops pedicellata* (Balanopaceae) is a tree of upland rainforest in the two archipelagos. Several Vanuatu–Fiji groups are in Vanuatu only on the southern islands, the part of the archipelago that originally lay next to Fiji.

The Vanuatu–Fiji centre of endemism and its biota have been rifted apart by the opening of the North Fiji basin along spreading ridges and transform margins, especially the Hunter and Fiji fracture zones (Fig. 7). Many groups in Vanuatu and Fiji would each have existed as metapopulations when the islands were adjacent, but the archipelagos and the metapopulations have since been rifted apart by ~800 km of sea floor spreading. Martin (2013) and Patriat et al. (2015) provided detailed reconstructions of the region, showing Fiji and Vanuatu rotating away from each other in the same way that double saloon doors open.

As discussed above, the Lau group in eastern Fiji was formerly adjacent to the Tonga arc, and there are five seed plants each endemic to Vanuatu, Fiji and Tonga (Smith, 1979–1996). This suggests that each of the five species represents a disrupted metapopulation.

In Vanuatu, islands such as Tanna are currently being built up by active volcanism, while older islands have disappeared in historical times by sliding down-slope into interarc rifts (Nunn et al., 2006). In Fiji, recent volcanism (beginning at 0.8 Ma) has built the island of Taveuni, 1241 m high, while 100 km to the south-east in the remnant arc of the Lau group there has been considerable subsidence. The distinctive montane endemics on Taveuni include the national flower, *tagimaucia* (*Medinilla waterhousei*: Melastomataceae). These endemics could have originated on the Lau group and colonized Taveuni before subsidence of the Lau islands led to the extinction of many higher-altitude groups there.

Metapopulation vicariance of marine groups at transform faults

Deep-sea hydrothermal vents, including black and white smokers, are located at zones of magmatism, usually at mid-ocean ridges. As with volcanic islands, the vents are ephemeral features. Nevertheless, the organisms found around the vents include local and regional endemics restricted to the habitat. These include the giant tube worm *Riftia* that forms columns up to 2.4 m tall and 4 cm wide. Many authors have accepted that organisms at the vents can display metapopulation dynamics, and that ancestral metapopulations on the mid-ocean ridges have undergone vicariance with displacement at transforms (Johnson et al., 2006; Plouviez et al., 2009; Vrijenhoek, 2010; Moalic et al., 2011). This research represents an exciting new synthesis of tectonics and marine biology. In contrast, the possible effects of transforms on reef groups and terrestrial groups in oceanic settings remain unexplored.

Different oceanic groups of plants and animals, including volcano weeds and hydrothermal marine taxa at the plate margins, intertidal groups around oceanic islands, and terrestrial groups on oceanic islands, all differ in the details of their ecology. Yet they all share metapopulation dynamics, and, if they are to survive, all require active magmatism and its products (such as hydrothermal vents, shallow reefs and islands). Likewise, groups in these different settings are all likely to undergo vicariance whenever the subduction zones are ruptured by transform faults.

Vicariance of oceanic metapopulations by sea floor spreading at mid-ocean ridges

Mid-ocean spreading ridges are divergent plate margins, and it is often accepted that they can cause vicariance between *continental* biotas. Yet their activity also separates biotas of *oceanic* islands and archipelagos, as in the North Fiji Basin and the Lau Basin. This process has also taken place at a much larger scale in the Pacific Basin as a whole. Its main spreading ridge, the East Pacific Rise, is generating the Pacific plate to its west and the Juan de Fuca, Cocos, Nazca and Antarctic plates to its east. The sea floor spreading would explain disjunction in many groups. One example comprises *Fitchia + Oparanthus* (Asteraceae) of SE Polynesia and the pair's sister, *Selleophytum + Narvalina* of Hispaniola (Mort et al., 2008; Heads, 2012, fig. 6-15). Others include a clade of *Fuchsia* (Onagraceae) in New Zealand and Tahiti, and its sister in South America (Heads, 2016, fig. 10.3); and *Apostates* (Asteracae) of Rapa Island and its sister the New World *Bahia* group (Baldwin and Wood, 2016).

Apart from causing divergence between plates, spreading ridges can themselves migrate, and the migrations of the East Pacific Rise and other spreading ridges in the Pacific are of particular significance for biology. For example, a broad belt of mid-ocean ridge basalts dated as Cretaceous extends for 7000 km from

Easter Island in SE Polynesia, north-west to the Tuamotu Plateau/Austral Islands, Line Islands, Mid-Pacific Mountains, and Shatsky Rise (1500 km east of Japan). (Samples from the oldest dated seamount in the Hawaiian–Emperor chain, the Detroit seamount, also show an isotopic signature indistinguishable from that of mid-ocean ridge basalt). This belt of on-ridge volcanism surrounds the off-ridge, intraplate volcanism of the Hawaiian chain and is likely to mark a former position of the East Pacific Rise (Heads, 2012, fig. 6-1).

Tectonics in the Pacific can be summarized as follows. The Pacific plate originated in the mid-Jurassic as a local feature near the modern Cook Islands, at a site where three ridges met at a triple junction (Smith, 2007). (Although the precursor of the modern Pacific Ocean has grown smaller through the Cretaceous and Cenozoic, the Pacific plate, along with its active margins, has expanded). One of the ridges at the triple junction, the East Pacific Rise, has migrated east, and eventually it collided with the western seaboard of North America (which was migrating west). Throughout the eastward migration of the ridge, the sea floor spreading taking place along it was probably an important mode of metapopulation vicariance in the terrestrial and reef biotas of the Pacific islands.

Large-scale volcanism has persisted in the central Pacific region since at least the Jurassic. At that time, the oldest of the Pacific large igneous provinces, the Shatsky Rise, began to be erupted in the region now occupied by French Polynesia. Plate movement has translated this plateau to its present position in deep sea east of Japan (Heads, 2012, fig. 6-1). The fossils and lithology at the plateau indicate shallow-water or subaerial volcanism during its emplacement (Sano et al., 2012). Following the eruption of the Shatsky Rise, volcanism continued in the central Pacific through the rest of the Cretaceous and the Cenozoic.

Dating clades

Vicariance is often rejected as a mode of differentiation between clades because the clades concerned are thought to be too young, that is, younger than the tectonic structures at their boundaries. Yet the dates are calibrated with fossil ages, and without adding *ad hoc* assumptions, this can only give minimum ages for clades. Actual clade ages are likely to be much older.

Fossil calibration of Bayesian timetrees: the problem of the priors

How much older than its oldest fossil can a group be? In Bayesian analyses, this amount is stipulated for a group before analysis, as a "prior", and it is used to calibrate the timetree. Priors are not observed or even calculated, they are simply imposed; they represent "expert knowledge", and these "prior-encoded beliefs vary from expert to expert" (Landis, 2017, p. 129). Experts in the Modern Synthesis tradition have assumed that a group is only a little older than its oldest fossil, and modern Bayesian clock studies maintain this view. However, there is no logical basis for it.

How *should* priors be selected? This is controversial, and "judgement of the degree to which fossil minima approximate divergence timing ... could be considered a dark art ..." (De Baets et al., 2016, p. 1). Naturally, the priors that are specified have a great effect on the results. "Errors in the time prior and in the rate prior can lead to *very precise but grossly inaccurate* time estimates ..." (dos Reis et al., 2016, p. 74). Kumar and Hedges (2016, p. 863) wrote: "we feel an urgent need for testing the accuracy and precision of third and fourth generation methods [for generating timetrees], including their robustness to misspecification of priors in the analysis of large phylogenies and data sets". To test the priors and the fossil-calibrated timetrees, these need to be compared with the results from another method. One other method of calibrating phylogenies is discussed next.

Tectonic–biogeographical calibration of timetrees

The tectonic–biogeographical method of dating clades correlates biogeographical–phylogenetic breaks with spatially coincident tectonic breaks. For example, differentiation between a group endemic to Vanuatu and one in Fiji could be dated to the separation of the two archipelagos at ~10 Ma. Differentiation between a group endemic to the main Pacific subduction zone and a sister on mainland Australia could be dated to the separation of the arc from the continent in the Cretaceous (Fig. 3). De Baets et al. (2016, p. 1) discussed the use of tectonic features to date clades and wrote:

> "Fossils only really provide minimum clade age constraints. In their place, phylogenetic trees can be calibrated by precisely dated geological events that have shaped biogeography ... Biogeographic calibrations are no panacea for the shortcomings of fossil calibrations, but their associated uncertainties can be accommodated ... Biogeographic and fossil calibrations are complementary, not competing, approaches to constraining molecular clock analyses."

Because the methods are independent, it is possible to compare and test fossil-calibrated clade ages against biogeography-calibrated ages.

The standard view of evolutionary chronology through the Phanerozoic is the fossil-calibrated timeline. Despite this, tectonic dating is now beginning to find favour. A recent review of evolution in the cabbage family, Brassicaceae, concluded:
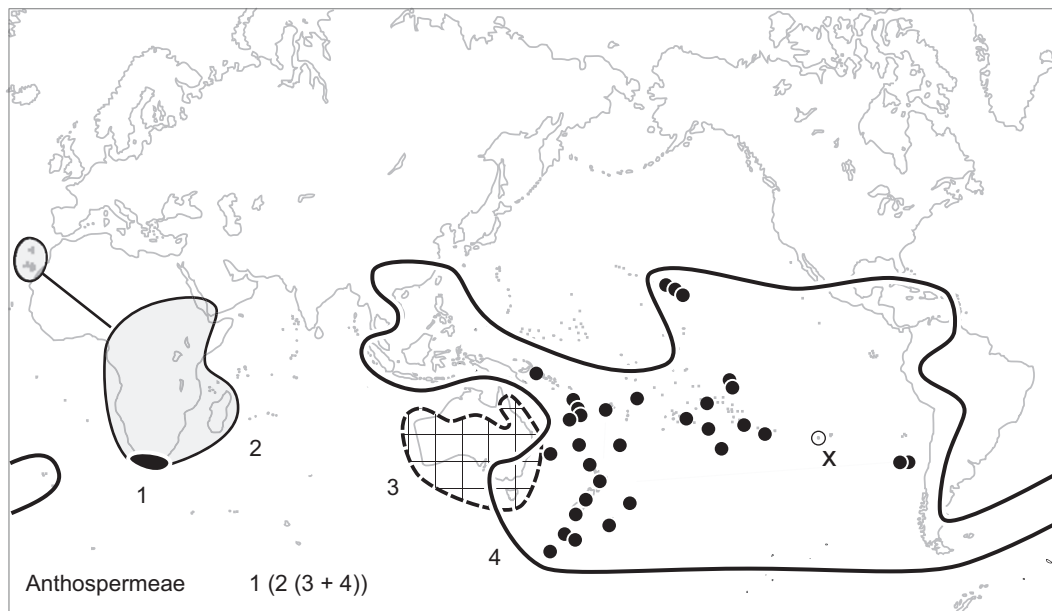
Fig. 8. Distribution of tribe Anthospermeae (Rubiaceae) and its four main clades. 1 = *Carpacoce*; 2 = Anthosperminae; 3 = Operculariinae; 4 = Coprosminae (Rydin et al., 2009). The phylogeny is: 1 (2 (3 + 4)). Black dots = localities of Coprosminae on Pacific islands east of Australia. Open circle with "x" = fossil pollen on Easter Island.

"We suggest that the few known fossils require a critical re-evaluation of phylogenetic and temporal assignments as a prerequisite for appropriate molecular dating analyses within the family. In addition, (palaeo)biogeographical calibrations, not explored so far in the family, should be integrated in a synthesis of various dating approaches ..." (Franzke et al., 2016, p. 554).

An analysis of New Zealand Brassicaceae using (palaeo)biogeographical calibrations is presented elsewhere (Heads, 2016).

Landis (2017, p. 129) argued that "fossil-free calibration methods are desperately needed", and he supported the use of tectonic–biogeographical dating:

"Many major paleogeographical events are dated, and since biogeographic processes depend on paleogeographical conditions, biogeographic dating may be used as an alternative or complementary method to fossil dating ... Biogeographic dating may present new opportunities for dating phylogenies for fossil-poor clades since the technique requires no fossils. This establishes that historical biogeography has untapped practical use..." (pp. 128, 142).

Spatial coincidence between geological structures and biological groups is widespread, and so there are many opportunities for testing tectonic–biogeographical calibration. These include groups on young oceanic islands.

Although Landis (2017) advocated testing tectonic methods of dating clades, Matzke (2015, p. 328) argued that using vicariance events for dating, "makes [the] inference circular". Nevertheless, it is not circular to make an assumption (Heads, 2016, p. 61). Authors using fossil ages to date clades also make critical assumptions (the Bayesian priors) about just how much older than its oldest fossil a clade can be.

A case-study: metapopulation vicariance in a continental and oceanic group

The tribe Anthospermeae (Rubiaceae) has a southern distribution, with the four main clades found, respectively, in South Africa (*Carpacoce*), Africa (Anthosperminae), Australia (Operculariinae) and the Pacific (Coprosminae). The distribution and phylogeny are shown in Fig. 8. The first three clades occur on continents, while the last inhabits continental lands and islands in the west Pacific, but also most of the high oceanic islands in the central and east Pacific.

The usual model of spatial evolution in the Anthospermeae proposes a centre of origin in Africa, because of the paraphyletic basal grade there (*Carpacoce* and Anthosperminae). With respect to time, Bayesian molecular clock analyses using fossil calibrations and stipulating narrow priors gave clade ages that are younger than the opening of the oceans (Wikström et al., 2015), thus supporting trans-oceanic dispersal. Likewise, in the Pacific group, Coprosminae, Cantley et al. (2016) rejected a vicariance origin for the island clades (including a Vanuatu–Fiji pair of sister species), as the current islands have never been joined to a continent or to each other

An alternative model for Anthospermeae proposes that the four main clades evolved more or less *in situ* by

vicariance of a pan-austral ancestor (Heads, in press). Subsequent dispersal of the subtribes has been restricted to South Africa and part of SE Australia, explaining the local overlap there. The basal node involves a break somewhere in or around South Africa, and this is followed by breaks in the Indian and Atlantic Oceans. The same sequence is seen in the breakup of Gondwana. The break in SE Australia between Operculariinae and Coprosminae coincides with the pre-drift rifting and uplift that took place in this part of Gondwana in the mid-Cretaceous, at ~100 Ma.

The Pacific contingent of Anthospermeae, the subtribe Coprosminae, has originated, persisted and evolved in its own particular sector by means of metapopulation survival and evolution, and there is no need for it to have invaded the region. There is no essential difference between the evolution of this largely oceanic group and that of its continental relatives in Africa and Australia.

Metapopulation vicariance in the south-west Pacific

The idea that the degree of an island's isolation is key to understanding its biota can be abandoned; instead, the main factor determining the biota of a site —whether insular or continental—is the site's *location*. The biotas of Vanuatu and Fiji, for example, have been determined by their development around convergent and divergent plate margins. In another case from Melanesia, the flora of New Caledonia has a "good claim to be considered the most remarkable in the world" (Thorne, 1965, p. 1). For example, it includes 43 endemic conifers (one parasitic) and several endemic angiosperm families. This is not explained by the island's distance from the nearest mainland or its size (18 600 km^2, about that of Wales or Massachusetts), but by its particular location in the SW Pacific, one of the most complex tectonic regions on Earth.

Many studies of groups in the SW Pacific have described spatial coincidence between well-documented biogeographical patterns and major tectonic features (reviewed in Heads, 2014, 2016). One important process in the construction of New Caledonia, New Guinea and New Zealand has been the repeated accretion of island arcs and intraplate seamounts to the mainlands, and this would have provided a rich source of terrestrial and marine groups. Fracturing of the accreted arcs into segments, both before and after accretion, will have led to metapopulation vicariance and endemism.

One recent study on Australasian birds suggested that:

> "Vicariance has not been considered to be a significant process of speciation in archipelagoes because many islands were never connected to other landmasses in the past (i.e. isolated

volcanic islands). However, at least two factors make vicariance a plausible and potentially common mode of speciation in island settings" (Weeks and Claramunt, 2014, p. 4).

The first factor that these authors cited was fluctuation in sea level. This can cause subdivision and reconnection of islands, and the process has been used to explain many biogeographic patterns. But the authors' second factor has been neglected. They wrote: " … most islands have not been completely isolated throughout their history, but are part of tectonically dynamic archipelagoes with *complex geological histories of fragmentation and collision*". (p. 4; italics added).

Weeks and Claramunt (2014) also stressed the great evolutionary power of vicariance. They observed that: "whereas a single long-distance dispersal event usually involves an individual lineage, a single vicariance event can affect entire biotas, potentially leading to multiple speciation events. As a consequence, even if not common, vicariance can be responsible for a substantial portion of speciation events in archipelagos" (p. 4).

Weeks and Claramunt (2014) were writing on birds in the SW Pacific, but vicariance mediated by tectonics has also been used to explain evolution there in invertebrates, such as oribatid mites. These have been interpreted as: "older taxa persisting on younger island through localised dispersal within island arc metapopulations … [The distribution pattern] is consistent with the hypothesis of differentiation of old metapopulations by vicariance as plates drifted apart, older volcanic islands subsided and new ones emerged … " (Colloff and Cameron, 2014, p. 272).

Conclusions

The long-term persistence of volcanic activity at particular centres means that terrestrial groups in oceanic settings could have survived there as metapopulations, more or less *in situ*, for tens of millions of years. It also means that they could have evolved *in situ*, and originated by vicariance with their relatives. Metapopulation vicariance in archipelagos of young islands is likely to occur with migration of an arc away from a continent, with the rifting of arcs at transform faults, with divergence at spreading ridges, with sea floor subsidence caused by sea floor cooling and volcanic loading, and with global change in sea level. With the massive subsidence of the Pacific plate, for example, many metapopulations that were widespread and mobile in the Mesozoic would have settled down through the Cenozoic into isolated clusters of immobile, more or less local endemics displaying different levels of differentiation.

In practice, many areas will have experienced more than one of the mechanisms that cause metapopulation

vicariance. For example, most intraplate archipelagos in the central Pacific will have been affected by rifting at mid-ocean ridges, sea floor subsidence, volcanic loading and Pleistocene sea level change.

As a result of metapopulation dynamics, many archipelagos host endemic species that are much older than any of the individual islands. Likewise, on continents, many regionally endemic species occur in habitat islands, such as mountains, new landslides, old termite mounds, leaves and puddles, that are all individually ephemeral. Yet these habitat islands are occupied by species that are much older than any *individual* mountain, landslide, termite mound, puddle or leaf.

The existence of metapopulations means there is no fundamental difference between the biogeographical evolution of land organisms on continents and those in oceanic habitats. Likewise, similar processes that govern terrestrial metapopulations on oceanic islands also determine the dynamics of reef organisms there, as the latter depend on barely submerged substrate—a patchy habitat in the oceans. A study of the widespread barnacle genus *Chthamalus* concluded: "Although individual islands are ephemeral ... regional endemics [can] survive and evolve as metapopulations ... [I]sland biogeographers should turn from studying the age and extrapolated ages of individual islands to re-examining the general history and evolution of subduction zones, spreading centers, fissures, arcs, back-arc basins and accreted terranes" (O'Riordan et al., 2010, p. 50).

Acknowledgements

References

Anderson, D.L., 2010. Hawaii, boundary layers and ambient mantle —geophysical constraints. J. Petrol. 52, 1547–1577.

Ashwal, L.D., Wiedenbeck, M., Torsvik, T.H., 2017. Archaean zircons in Miocene oceanic hotspot rocks establish ancient continental crust beneath Mauritius. Nat. Commun. 8, 1–9.

Baldwin, B.G., Wood, K.R., 2016. Origin of the Rapa endemic genus *Apostates*: revisiting major disjunctions and evolutionary conservatism in the *Bahia* alliance (Compositae: Bahieae). Taxon 65, 1064–1080.

Beverley, S.M., Wilson, A.C., 1985. Ancient origin for Hawaiian Drosophilinae inferred from protein comparisons. Proc. Natl Acad. Sci. USA 82, 4753–4757.

Bonneville, A., 2009. French Polynesia, geology. In: Gillespie, R.G., Clague, D.A. (Eds.), Encyclopedia of Islands. University of California Press, Berkeley, CA, pp. 338–343.

Borregaard, M.K., Amorim, I.R., Borges, P.A.V., Cabral, J.S., Fernández-Palacios, J.M., Field, R., Heaney, L.R., Kreft, H., Matthews, T.J., Olesen, J.M., Price, J., Rigal, F., Steinbauer, M.J., Triantis, K.A., Valente, L., Weigelt, P., Whittaker, R.J.,

2017. Oceanic island biogeography through the lens of the general dynamic model: assessment and prospect. Biol. Rev. 92, 830–853.

Cantley, J.T., Markey, A.S., Swenson, N.G., Keeley, S.C., 2016. Biogeography and evolutionary diversification in one of the most widely distributed and species rich genera of the Pacific. AoB Plants 8, plw043.

Carr, L.M., McLenachan, P.A., Waddell, P.J., Gemmell, N.J., Penny, D., 2015. Analyses of the mitochondrial genome of *Leiopelma hochstetteri* argues against the full drowning of New Zealand. J. Biogeogr. 42, 1066–1076.

Clague, D.A., 1996. The growth and subsidence of the Hawaiian-Emperor volcanic chain. In: Keast, A., Miller, S. (Eds.), The Origin and Evolution of Pacific Island Biotas, New Guinea to Eastern Polynesia. SPB Academic Publishing, Amsterdam, pp. 35–50.

Colley, H., Hindle, W.H., 1984. Volcano-tectonic evolution of Fiji and adjoining marginal basins. Geol. Soc. London, Special Publ. 16, 151–162.

Colloff, M.J., Cameron, S.L., 2014. Beyond Moa's Ark and Wallace's Line: extralimital distribution of new species of *Austronothrus* (Acari, Oribatida, Crotoniidae) and the endemicity of the New Zealand oribatid mite fauna. Zootaxa 3780, 263–281.

Cronin, S.J., Ferland, M.A., Terry, T.P., 2003. Nabukelevu volcano (Mt. Washington), Kadavu – a source of hitherto unknown volcanic hazard in Fiji. J. Volcanol. Geothermal Res. 131, 371–396.

Darwin, C., 1859. On the Origin of Species, 1st edn. John Murray, London.

De Baets, K., Antonelli, A., Donoghue, P.C., 2016. Tectonic blocks and molecular clocks. Philos. Trans. R. Soc. Lond. B Biol. Sci. 371, 20160098.

Ebach, M.C., Williams, D.M., 2016. Dispersalism and neodispersalism. In: Williams, D., Schmitt, M., Wheeler, Q. (Eds.), The Future of Phylogenetic Systematics: The Legacy of Willi Hennig. Cambridge University Press, Cambridge UK, pp. 286–329.

Foulger, G.R., Panza, G.F., Artemieva, I.M., Bastow, I.D., Cammarano, F., Evans, J.R., Hamilton, W.B., Julian, B.R., Lustrino, M., Thybo, H., Yanovskaya, T.B., 2013. Caveats on tomographic images. Terra Nova 25, 259–281.

Franzke, A., Koch, M.A., Mummenhoff, K., 2016. Turnip time travels: age estimates in Brassicaceae. Trends Plant Sci. 21, 554–561.

Gillespie, R.G., Roderick, G.K., 2002. Arthropods on islands: colonization, speciation, and conservation. Annu. Rev. Entomol. 47, 595–632.

Gilpin, M.E., Hanski, I.A. (Eds.), 1997. Metapopulation Biology: Ecology, Genetics, and Evolution. Academic Press, San Diego, CA.

Hamilton, W.B., 2011. Plate tectonics began in Neoproterozoic time, and plumes from deep mantle have never operated. Lithos 123, 1–20.

Hanski, I.A., 1999. Metapopulation Ecology. Oxford University Press, Oxford, UK.

Hanski, I.A., 2010. Island biogeography and metapopulations. In: Losos, J.B., Ricklefs, R.E. (Eds.), The Theory of Island Biogeography Revisited. Princeton University Press, Princeton, NJ, pp. 186–213.

Hanski, I.A., Gaggiotti, O.E. (Eds.), 2004. Ecology, Genetics and Evolution of Metapopulations. Elsevier, Burlington, MA.

Heads, M., 2006. Seed plants of Fiji: an ecological analysis. Biol. J. Linn. Soc. 89, 407–431.

Heads, M., 2008. Panbiogeography of New Caledonia, southwest Pacific: basal angiosperms on basement terranes, ultramafic endemics inherited from volcanic arcs, and old taxa endemic to young islands. J. Biogeogr. 35, 2153–2175.

Heads, M., 2011. Old taxa on young islands: a critique of the use of island age to date island-endemic clades and calibrate phylogenies. Syst. Biol. 60, 204–218.

Heads, M., 2012. Molecular Panbiogeography of the Tropics. University of California Press, Berkeley, CA.

Heads, M., 2014. Biogeography of Australasia: A Molecular Analysis. Cambridge University Press, Cambridge, UK.

Heads, M., 2016. Biogeography and Evolution in New Zealand. Taylor & Francis/CRC, Boca Raton, FL.

Heads, M., in press. Metapopulation vicariance in the Pacific genus *Coprosma* (Rubiaceae) and its Gondwanan relatives. Aust. Syst. Bot.

Hillier, J.K., Watts, A.B., 2005. Relationship between depth and age in the North Pacific Ocean. J. Geophys. Res. 110, B02405. https://doi.org/10.1029/2004jb003406

Holland, B., 2012. If the conceptual straitjacket fits, chances are, you're already wearing it. Front. Biogeogr. 4, 144–147.

IUCN, 2016. The IUCN redlist of threatened species. www.iucnredlist.org

Johnson, S.B., Young, C.R., Jones, W.J., Warén, A., Vrijenhoek, R.C., 2006. Migration, isolation, and speciation of hydrothermal vent limpets (Gastropoda; Lepetodrilidae) across the Blanco Transform Fault. Biol. Bull. 210, 140–157.

Kumar, S., Hedges, S.B., 2016. Advances in time estimation methods for molecular data. Mol. Biol. Evol. 33, 863–869.

Landis, M.J., 2017. Biogeographic dating of speciation times using paleogeographically informed processes. Syst. Biol. 66, 128–144.

Le Péchon, T., Dai, Q., Zhang, L.B., Gao, X.F., Sauquet, H., 2015. Diversification of Dombeyoideae (Malvaceae) in the Mascarenes: old taxa on young islands? Int. J. Plant Sci. 176, 211–221.

Lomolino, M.V., Riddle, B.R., Whittaker, R.J., Brown, J.H., 2010. Biogeography, 4th edn. Sinauer, Sunderland, MA.

Lovette, I.J., Arbogast, B.S., Curry, R.I., Zink, R.M., Botero, C.A., Sullivan, J.P., Talaba, A.L., Harris, R.B., Rubenstein, D.R., Ricklefs, R.E., Bermingham, E., 2012. Phylogenetic relationships of the mockingbirds and thrashers (Aves: Mimidae). Mol. Phylogenet. Evol. 63, 219–229.

MacArthur, R.H., Wilson, E.O., 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, NJ.

Martin, A.K., 2013. Double-saloon-door tectonics in the North Fiji Basin. Earth Planet. Sci. Lett. 374, 191–203.

Matzke, N.J., 2015. Review of "Biogeography of Australasia: A Molecular Analysis" by Michael Heads. Q. Rev. Biol. 90, 327–328.

Moalic, Y., Desbruyères, D., Duarte, C.M., Rozenfeld, A.F., Bachraty, C., Arnaud-Haond, S., 2011. Biogeography revisited with network theory: retracing the history of hydrothermal vent communities. Syst. Biol. 61, 127–137.

Monaghan, M.T., Balke, M., Pons, J., Vogler, A.P., 2006. Beyond barcodes: complex DNA taxonomy of a South Pacific Island radiation. Proc. R. Soc. B Lond. Biol. Sci. 273, 887–893.

Mort, M.E., Randle, C.P., Kimball, R.T., Tadesse, M., Crawford, D.J., 2008. Phylogeny of Coreopsideae (Asteraceae) inferred from nuclear and plastid DNA sequences. Taxon 57, 109–120.

Nunn, P.D., Baniala, M., Harrison, M., Geraghty, P., 2006. Vanished islands in Vanuatu: new research and a preliminary geohazard assessment. J. R. Soc. N. Z. 36, 37–50.

O'Grady, P.M., Bennett, G.M., Funk, V.A., Altheide, T.K., 2012. Retrograde biogeography. Taxon 61, 699–705.

O'Riordan, R.M., Power, A.M., Myers, A.A., 2010. Factors, at different scales, affecting the distribution of species of the genus *Chthamalus* Ranzani (Cirripedia, Balanomorpha, Chthamaloidea). J. Exp. Mar. Biol. Ecol. 392, 46–64.

Patriat, M., Collot, J., Danyushevsky, L., Fabre, M., Meffre, S., Falloon, T., Rouillard, P., Pelletier, B., Roach, M., Fournier, M., 2015. Propagation of back-arc extension into the arc lithosphere in the southern New Hebrides volcanic arc. Geochem. Geophys. Geosyst. 16, 3142–3159.

Pindell, J.L., Kennan, L., 2009. Tectonic evolution of the Gulf of Mexico, Caribbean and northern South America in the mantle reference frame: an update. Geol. Soc. London Special Publ. 328, 1–55.

Plouviez, S., Shank, T.M., Faure, B., Daguin-Thiébaut, C., Viard, F., Lallier, F.H., Jollivet, D., 2009. Comparative phylogeography among hydrothermal vent species along the East Pacific Rise reveals vicariant processes and population expansion in the south. Mol. Ecol. 18, 3903–3917.

van der Pluijm, B.A., Marshak, M., 2004. Earth Structure: An Introduction to Structural Geology and Tectonics, 2nd edn. Norton, New York.

Price, J.P., Clague, D.A., 2002. How old is the Hawaiian biota? Geology and phylogeny suggest recent divergence Proc. R. Soc. B Lond. Biol. Sci. 269, 2429–2435.

dos Reis, M., Donoghue, P.C., Yang, Z., 2016. Bayesian molecular clock dating of species divergences in the genomics era. Nat. Rev. Genet. 17, 71–80.

Rose, J., Koppers, A.A.P., 2014. An evaluation of the complex age progression along the Cook-Austral Islands using high-resolution $^{40}Ar/^{39}Ar$ incremental heating ages. In: *American Geophysical Union Fall Meeting 2014 (San Francisco)*. Abstract #DI43A-4360. https://ui.adsabs.harvard.edu/#abs/2014AGUFMDI43A4360R/abstract

Rydin, C., Razafimandimbison, S.G., Khodabandeh, A., Bremer, B., 2009. Evolutionary relationships in the Spermacoceae alliance (Rubiaceae) using information from six molecular loci: insights into systematic affinities of *Neohymenopogon* and *Mouretia*. Taxon 58, 793–810.

Sano, T., Shimizu, K., Ishikawa, A., Senda, R., Chang, Q., Kimura, J.I., Widdowson, M., Sager, W.W., 2012. Variety and origin of magmas on Shatsky Rise, northwest Pacific Ocean. Geochem. Geophys. Geosyst. 13(8), 1–25. https://doi.org/10.1029/2012gc004235

Schellart, W.P., Lister, G.S., Toy, V.G., 2006. A Late Cretaceous and Cenozoic reconstruction of the Southwest Pacific region: tectonics controlled by subduction and slab rollback processes. Earth-Sci. Rev. 76, 191–233.

Schmalfuss, H., 2003. World catalog of terrestrial isopods (Isopoda: Oniscidea). Stuttgarter Beitr. Naturk. Ser. A 654, 1–341.

Smith, A.C., 1979–1996. Flora Vitiensis Nova: A New Flora of Fiji (Spermatophytes only). 6 vols. Pacific Tropical Botanical Garden, Kauai, Hawaii.

Smith, A.D., 2007. A plate model for Jurassic to Recent intraplate volcanism in the Pacific Ocean basin. Geol. Soc. Am. Spec. Pap. 430, 471–495.

Spalik, K., Banasiak, Ł., Feist, M.A.E., Downie, S.R., 2014. Recurrent short-distance dispersal explains wide distributions of hydrophytic umbellifers (Apiaceae tribe Oenantheae). J. Biogeogr. 41, 1559–1571.

Sykes, W.R., 1998. *Scaevola gracilis* (Goodeniaceae) in the Kermadec Islands and Tonga. N. Z. J. Bot. 36, 671–674.

Telegraph [London], 2015. First photographs emerge of new Pacific island off Tonga. www.telegraph.co.uk/news/worldnews/australiaandthepacific/tongafrenchpolynesia/11463853/First-photographs-emerge-of-new-Pacific-island-off-Tonga.html

Thorne, R.F., 1965. Floristic relationships of New Caledonia. Univ. Iowa Studies Nat. Hist. 20(7), 1–14.

Triantis, K.A., Whittaker, R.J., Fernández-Palacios, J.M., Geist, D.J., 2016. Oceanic archipelagos: a perspective on the geodynamics and biogeography of the world's smallest biotic provinces. Front. Biogeogr. 8.2, e29605. pp. 1-9.

Vrijenhoek, R.C., 2010. Genetic diversity and connectivity of deep-sea hydrothermal vent metapopulations. Mol. Ecol. 19, 4391–4411.

Weeks, B.C, Claramunt, S., 2014. Dispersal has inhibited avian diversification in Australasian archipelagoes. Proc. R. Soc. B 281, 20141257.

Whittaker, R.J., Fernández-Palacios, J.M., 2007. Island Biogeography: Ecology, Evolution, and Conservation. 2nd edn. Oxford University Press, Oxford, UK.

Whittaker, R.J., Triantis, K.A., Ladle, R.J., 2008. A general dynamic theory of oceanic island biogeography. J. Biogeogr. 35, 977–994.

Whittaker, R.J., Triantis, K.A., Ladle, R.J., 2010. A general dynamic theory of oceanic island biogeography: extending the MacArthur–Wilson theory to accommodate the rise and fall of volcanic islands. In: Losos, J.B., Ricklefs, R.E. (Eds.), The Theory of Island Biogeography Revisited. Princeton University Press, Princeton, NJ, pp. 88–115.

Wikström, N., Kainulainen, K., Razafimandimbison, S.G., Smedmark, J.E.E., Bremer, B., 2015. A revised time tree of the asterids: establishing a temporal framework for evolutionary studies of the coffee family (Rubiaceae). PLoS ONE 10, e0126690. pp. 1-26.

Zhong, S., Ritzwoller, M., Shapiro, N., Landuyt, W., Huang, J., Wessel, P., 2007. Bathymetry of the Pacific plate and its implications for thermal evolution of lithosphere and mantle dynamics. J. Geophys. Res. 112, B06412. https://doi.org/10.1029/2006jb004628.