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**THE REAL WORLD STRUCTURE OF BIODIVERSITY ILLUSTRATED BY THE
BIOGEOGRAPHY AND SYSTEMATICS OF SOME PLANTS, LIZARDS, BIRDS,
AND DRAGONFLIES**

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The real world structure of biodiversity illustrated by the biogeography and systematics of some plants, lizards, birds, and dragonflies

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Abstract

Examples are drawn from regional animal and plant distributions to show how distributions of taxa are spatially correlated with tectonic structures of the Earth. Spatial correlations of distributions with Earth's tectonics are illustrated for the Jurassic Lebombo-Mwenetzi monocline, the plate boundary between Indo-Australia and the Pacific, and the East Pacific Rise. These examples illustrate how biodiversity has a coherent spatial and phylogenetic structure that is not confined to the biological composition of organisms alone. This tectonic relationship is evidence for the global structure of biodiversity being directly derived from the geography of ancestral distributions in the Mesozoic, and shows how some distributional boundaries have remained geographically stable for tens of millions of years. The spatial and tectonic correlations show that biodiversity is phylogeny *and* biogeography that, together with their correlation with global tectonics, makes biodiversity an empirical evolutionary reality.

Keywords

Cryptoblepharus, *Dianella*, conservation, evolution, geology, *Hemicordulia*, Lebombo-Mwenetzi monocline, Mesozoic, *Monarcha*, systematics, vicariance

Introduction

Biodiversity is often equated with simple species diversity, but the spatial distribution of clades (biogeography) contributes as much to the global structure, or organization, of biodiversity as phylogeny and taxonomy. The combination of biogeography and taxonomy is necessary in order to interpret the evolutionary structure of biodiversity. By mapping distributions of taxa, it is possible to identify the spatial organization of biodiversity and to compare this with Earth's geological structure and history. This approach was initiated many years ago (Croizat 1958, 1964) and continues to be developed and applied (e.g. Heads 2012a, 2014, 2017a, 2019; Ferretti *et al.* 2014a, b; del Rio *et al.* 2015; Grehan 2017, 2019; Grehan & Mielke 2018; Morrone 2018; Santos-Silva *et al.* 2018; Mielke *et al.* 2020; Heads & Grehan 2021). Distribution maps provide empirical data that is informative about the evolution of biodiversity (Craw *et al.* 1999). By mapping the distributions of sister taxa in relation to geology, it is possible to identify tectonic correlations that provide information on the evolution of biodiversity.

It may seem obvious that the organizational structure of biodiversity is made up of the biogeography as well as the systematics of organisms, but this understanding is not evident in prevailing definitions of biodiversity. For example, the National Geographic Society (2021) limits its definition to “the variety of living species on Earth.” The United Nations Environment Program (2021) identifies biodiversity as “the variability among living organisms from all sources including, *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are a part; this includes diversity within species, between species and of ecosystems”. The same outlook includes at least some government programs. For example, the New Zealand Department of Conservation (2021) regards biodiversity as an abbreviation for ‘biological diversity’ that “simply means the variety of life on earth (sic)” These definitions do not acknowledge the geographic structure of biodiversity.

By restricting the meaning of biodiversity to purely taxonomic phenomena, one could

theoretically preserve it simply by storing samples of all the world's living taxa in a zoo, arboretum, or laboratory. But biodiversity has a natural existence beyond the organisms themselves. What is this 'natural existence' and how is it to be documented? Darwin (1859, p. 1) anticipated this question when writing that he was "... much struck with certain facts in the distribution of the organic beings inhabiting South America, and in the geological relations of the present to the past inhabitants of that continent. These facts...seemed to throw some light on the origin of species – that mystery of mysteries...".

Darwin realized, in a nascent way, that different organisms existed in geographic space, and that, in combination with geology, these differences provided information on the course of evolution. While the systematic relationships of taxa have long been recognized as a sequence of evolutionary history, the geography of taxa as an empirical source of historical data has largely been overlooked and geography reduced to the status of a stage or container of evolution, rather than being an integral part of it. This popular oversight overlooks the fact that there is another long-standing tradition that recognizes biodiversity as the result of evolutionary processes taking place in space and time, as well as in biological form; essentially, evolution = space + time + form. This synthesis of phytogeography, zoogeography and geology is known as panbiogeography (Croizat 1958).

Biodiversity and tectonics

There is now a massive amount of published literature documenting the reality that different taxa share spatial patterns of distribution, regardless of their ability to move about (i.e. whether they are 'good' or 'poor' dispersers). Hundreds of taxa have now been shown to have distribution ranges or boundaries that span or border tectonic structures such as plate boundaries (spreading ridges, subduction zones and transforms), other faults, folds, and belts of magmatism and metamorphism (Craw *et al.* 1999, Heads 2012). These correlations form one of the most prominent facts of the world's biodiversity, and they indicate that these tectonic structures are responsible for geologically mediated isolation within the ancestral range. The following examples illustrate how geographic and phylogenetic analysis of biodiversity demonstrates the spatial correlation of animal and plant distributions with Earth tectonics as a primary fact of evolutionary biodiversity.

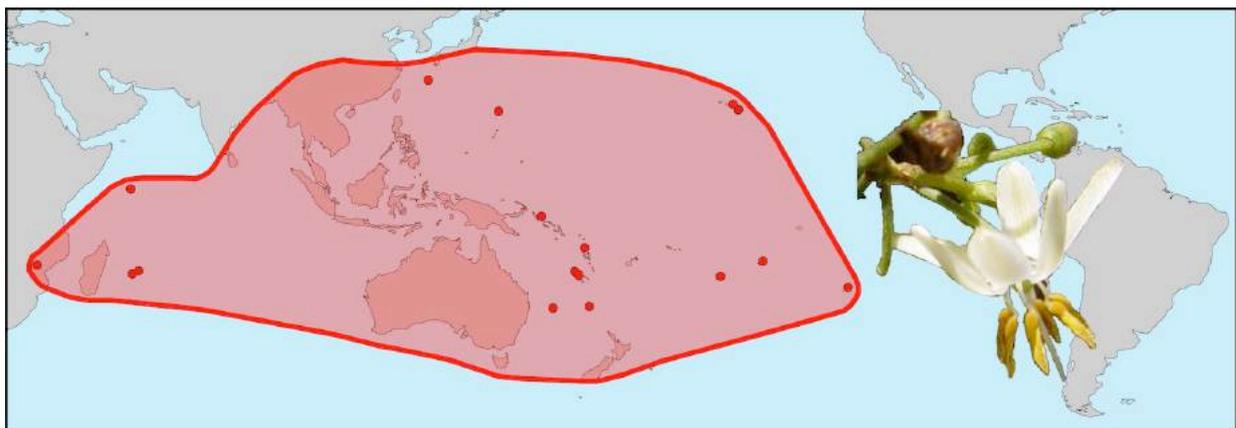


Fig. 1. Distribution of *Dianella*. Isolated island localities as red circles. Simplified from Muscat *et al.* (2019).

Geographically isolated populations and global biodiversity

The plant genus *Dianella* (Asphodelaceae) is widespread, ranging between southern Africa and the central Pacific (Fig. 1) (Muscat *et al.* 2019). The genus spans more than half the world and includes three continents, while being noticeably absent from the New World and most of Africa. The distribution has a western boundary in southern Africa and an eastern boundary in the central Pacific. These boundaries would be of no scientific interest if geographic

distribution were uninformative and simply the result of chance. The western and eastern boundaries of *Dianella* are shared by large numbers of other taxa, which would suggest that the common patterns are indeed the result of a shared historical mechanism.

The western boundary of *Dianella* occurs in eastern Zimbabwe. There is no obvious ecological correlation, but the locality does coincide with a major geological structure, a rifted margin known as the Lebombo-Mwenetzi monocline. This extends from eastern South Africa to eastern Zimbabwe (Fig. 2). The monocline is part of the Karoo large igneous province and formed along the western edge of a tectonic rift separating East Antarctica from southern Africa, beginning in the Jurassic (about 182 Ma) (Klausen 2009). The boundary of *Dianella* at the monocline is consistent with this region being at the boundary of the ancestral distribution for *Dianella*, resulting in some populations being 'trapped' within Africa following rifting. The present-day inland location is a consequence of the population remaining localized, even though an extensive area of sedimentary rock forming the Mozambique lowlands now separates the monocline from the Indian Ocean.

The spatial correlation of *Dianella* with the Lebombo-Mwenetzi monocline cannot be justified as the result of chance, because the relationship is evident in large numbers of other animal and plant taxa with completely different ecology, including other groups with trans-oceanic affinities. For example, in plants, the Lebombo-Mwenetzi monocline is correlated with differentiation between the subfamilies Rutoideae and Aurantioideae (Rutaceae) (Heads 2012: fig. 9-2), between the *Vepris-Flindersia* and Diosmeae-Galipeeae clades of Rutaceae (Heads 2012: fig. 9-3), and between Canellaceae and Winteraceae (Heads 2012: fig. 9.5). Each of these distributions can be explained by vicariance of a widespread Gondwanan ancestor resulting from formation of the Indian Ocean. The range limit of *Dianella* is an example of a corresponding tectonic boundary that is consistent with a Gondwanan age for the ancestor. As with plants, there are also innumerable examples of animals with African-east Asian/Australian distributions, some involving just eastern Africa, or Madagascar and other islands in the Indian Ocean. Two Indian Ocean animal groups associated with the Lebombo-Mwenetzi monocline are the lizard genus *Cryptoblepharus* (Scincidae) (Fig. 3), and the dragonfly genus *Hemicordulia* (Corduliidae) (Fig. 4).

Most species of *Cryptoblepharus* occupy a geographic range between eastern Africa/Madagascar and Australasia/southeastern Asia/Western Pacific (Fig. 3), while one species spans the Pacific basin. In Africa, the southern distributional boundary of *C. africanus* is close to the southern limits of the Lebombo monocline, but unlike *Dianella*, the lizards have not become 'stranded' inland following sedimentation east of the original Lebombo-Mwenetzi coastline. Instead, it would appear that the coastal range was maintained as the coastline expanded east into the Indian Ocean, following the separation of Africa and Antarctica (Fig. 4). The dragonfly genus *Hemicordulia* has an African-western Pacific distribution and shares a presence in Madagascar and Mauritius with *Cryptoblepharus* (Fig. 5). The African species occupies an inland range along the East African Rift which formed by about 30 Ma (Roberts *et al.* 2012), and a coastal population just south of the Lebombo monocline.

The distributions of *Dianella*, *Cryptoblepharus*, and *Hemicordulia* suggest that a tectonic rift forming along the Lebombo-Mwenetzi monocline during the early Jurassic caused the geographic boundaries of differentiation in many groups. This correlation is evidence that these and other taxa evolved at this time, even if this age may precede their earliest fossil record.

This method of biogeographic-tectonic correlation for the western boundaries of these taxa is also applicable to their eastern distributional limits and relationships in the Pacific. It is usually assumed that all Pacific taxa descended from waifs and strays from continental regions.

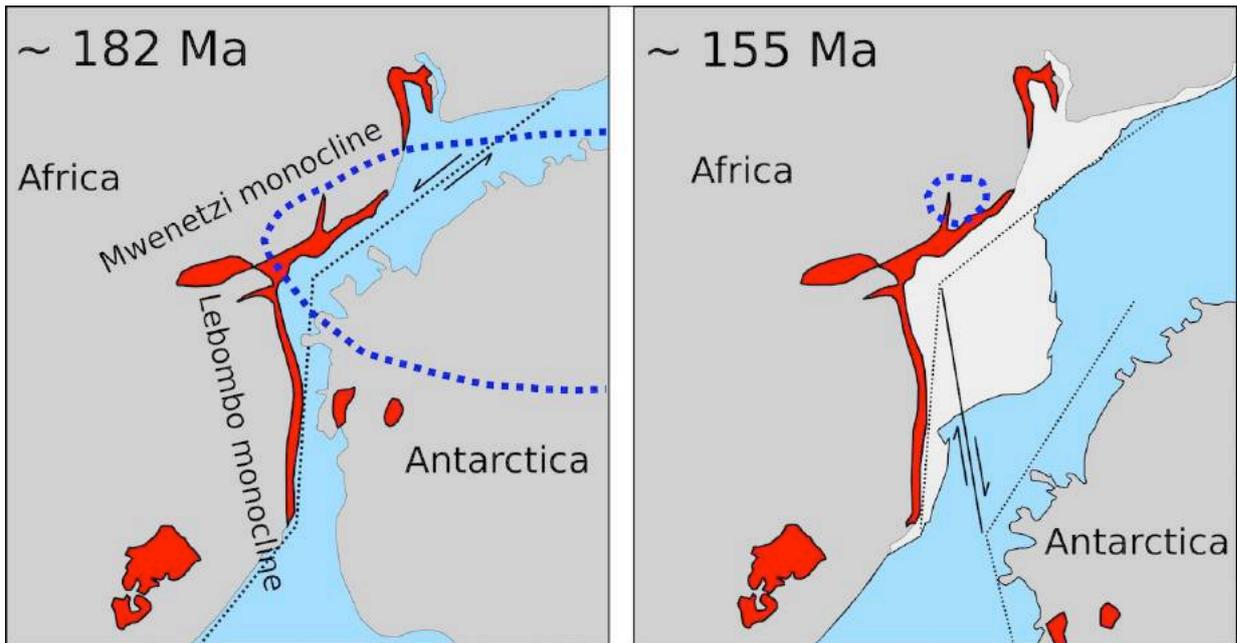


Fig. 2. Left – hypothetical western range limit of *Dianella* about 182 Ma (blue dashed line). Right – pocket of surviving *Dianella* (blue dashed line) following continental separation and deposition of new sediments (pale grey) forming the Mozambique lowlands. Red – Karoo lavas (Drakensberg Group). Modified from Klausen (2009).

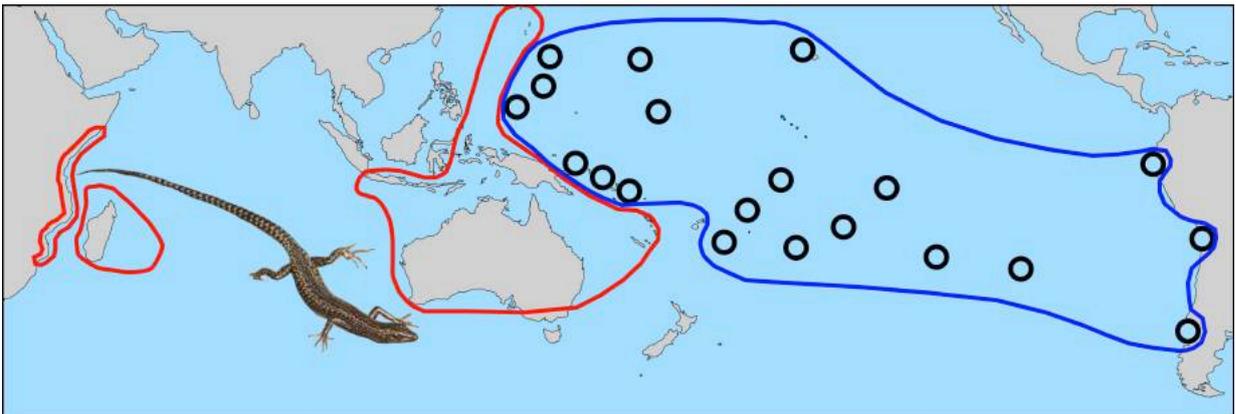


Fig. 3. Distribution of *Cryptoblepharus*. Blue outline – Pacific species *C. poecilopleurus* (Wiegmann 1836) with individual localities marked as circles. Red outline – all other species. Distribution data from Branch (1998), Horner (2007), <https://reptile-database.reptarium.cz/>

However, there is no empirical evidence for that view (Heads 2012a). Absence of continental landscapes does not mean that the Pacific cannot support its own biota. Individual oceanic islands may be ephemeral, but clades can persist in the region in the form of metapopulations spanning multiple islands that have been continuously forming since the origin of the basin. Taxa survive through the colonization of new islands, as older islands erode and submerge below sea level. This is the same ecological process seen in continental organisms that occupy ephemeral habitats and persist by continually colonizing new habitats (Heads 2017b, 2017c). As with continental organisms, taxa occupying the Pacific can maintain widespread ancestral ranges that may be subject to disruption or dislocation by tectonic processes.

The distribution of *Cryptoblepharus poecilopleurus* ranges across islands in the Pacific basin as well as the adjacent continental landmass of South America. The boundaries of this distribution do not correspond with any pattern of geographic isolation, but the localities for this species occur either on the plate, or along its eastern and western boundaries. The western plate boundary also demarcates allopatry between *C. poecilopleurus* and other species of the genus, except for local overlap on the island of Palau (Fig.6).

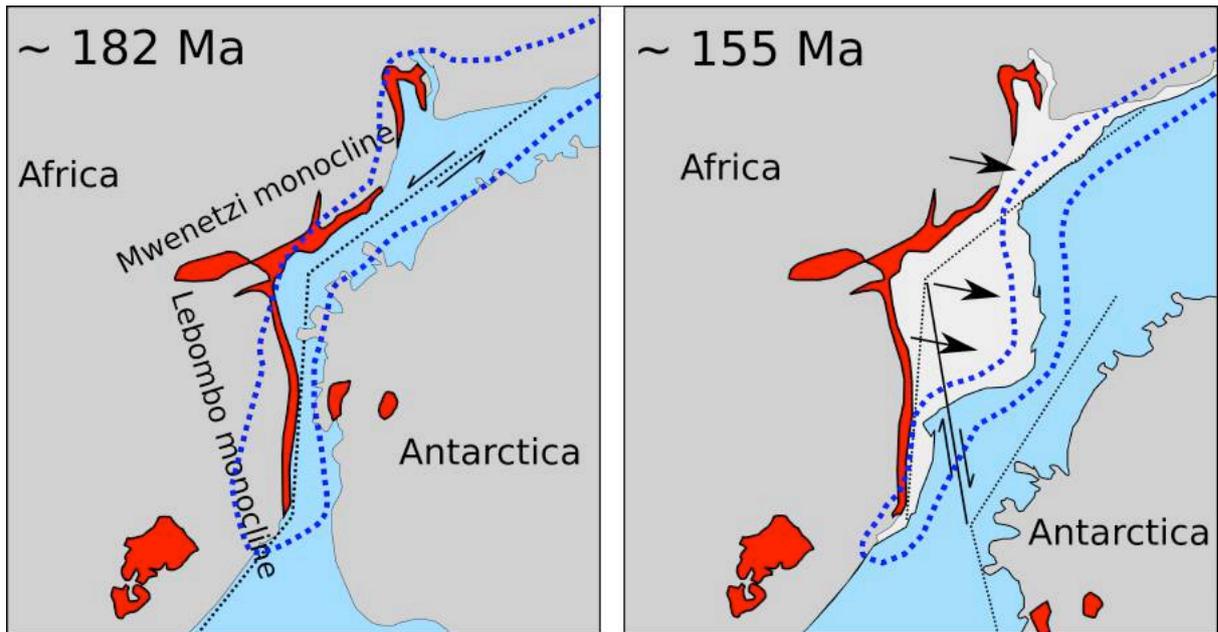


Fig. 4. Left – hypothetical southern range of African *Cryptoblepharus* along the coastal rift valley as Africa separates from Antarctica about 182 Ma; right – present day coastal range of *Cryptoblepharus* expanding east (black arrows) onto exposed sedimentary strata (pale grey) that form the Mozambique lowlands. Red – Karoo lavas. Geological model from Klausen (2009).

The distribution of *Dianella* does not share the trans-Pacific distribution of *Cryptoblepharus*. Instead, its eastern boundary is at the Hawaiian and Easter Islands. This boundary is probably not an artifact of chance dispersal, as the distributions of many other taxa also share a similar boundary. One example is a clade of flycatcher birds (Monarchidae) comprising three allopatric subclades (Fig. 7), with a Pacific group (No. 1) being the sister of two other allopatric subclades (Nos. 2 + 3). According to Filardi & Moyle (2005, p. 217) “These results [for the flycatchers] strongly support a recent, rapid sequence of colonization and diversification across all major archipelagos in the Pacific, followed by subsequent recolonization of Australia and New Guinea.” However, the geographic and systematic evidence does not support this assertion. Filardi & Moyle (2005) assume chance dispersal is responsible, as if waifs and strays are somehow blown around in such a way that they end up in different localities to those of their sister groups. This presents the classic paradox of using chance dispersal to explain the origin of allopatry. Localities are supposed to be simultaneously accessible and isolated. The confusion is removed if dispersal is recognized as an empirically observable ecological process that explains the overlap of clades, but not their divergence. In this context, the eastern distributional boundary of the *Hemicordulia* dragonflies does not extend quite so far into the central Pacific (Fig.5), but represents a more restricted range of metapopulation persistence within the Pacific basin.

While ecological dispersal can modify the range of a species, it is the impact of geological and climatic isolating mechanisms that generates allopatric divergence within the ancestral range and brings about the range of a group at its origin (Croizat 1958). In this context, the ancestral distribution can be reconstructed by combining the ranges of the allopatric descendants. Some or all of these descendants may, in time, be subject to range expansion which will result in partial or complete range overlap. This vicariance model of evolutionary differentiation does not set up contradictions between dispersal and divergence. Explaining divergence by unobservable and unique migrations that are uncorrelated with any other biological or geological factor is not based on empirical evidence and is not necessary to explain allopatry (Heads 2012a).

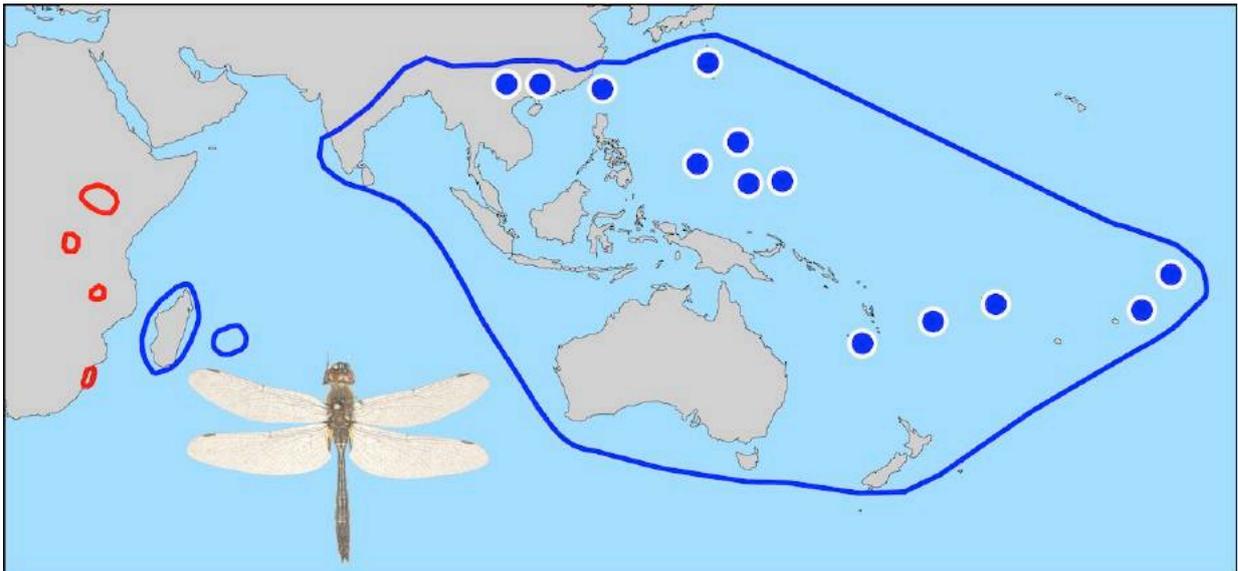


Fig. 5. Distribution of the dragonfly *Hemicordulia*. Based on data from Dijkstra (2007: fig. 18) and Marinov (2012, pers. comm. 2021). Island localities in the Pacific as blue circles.

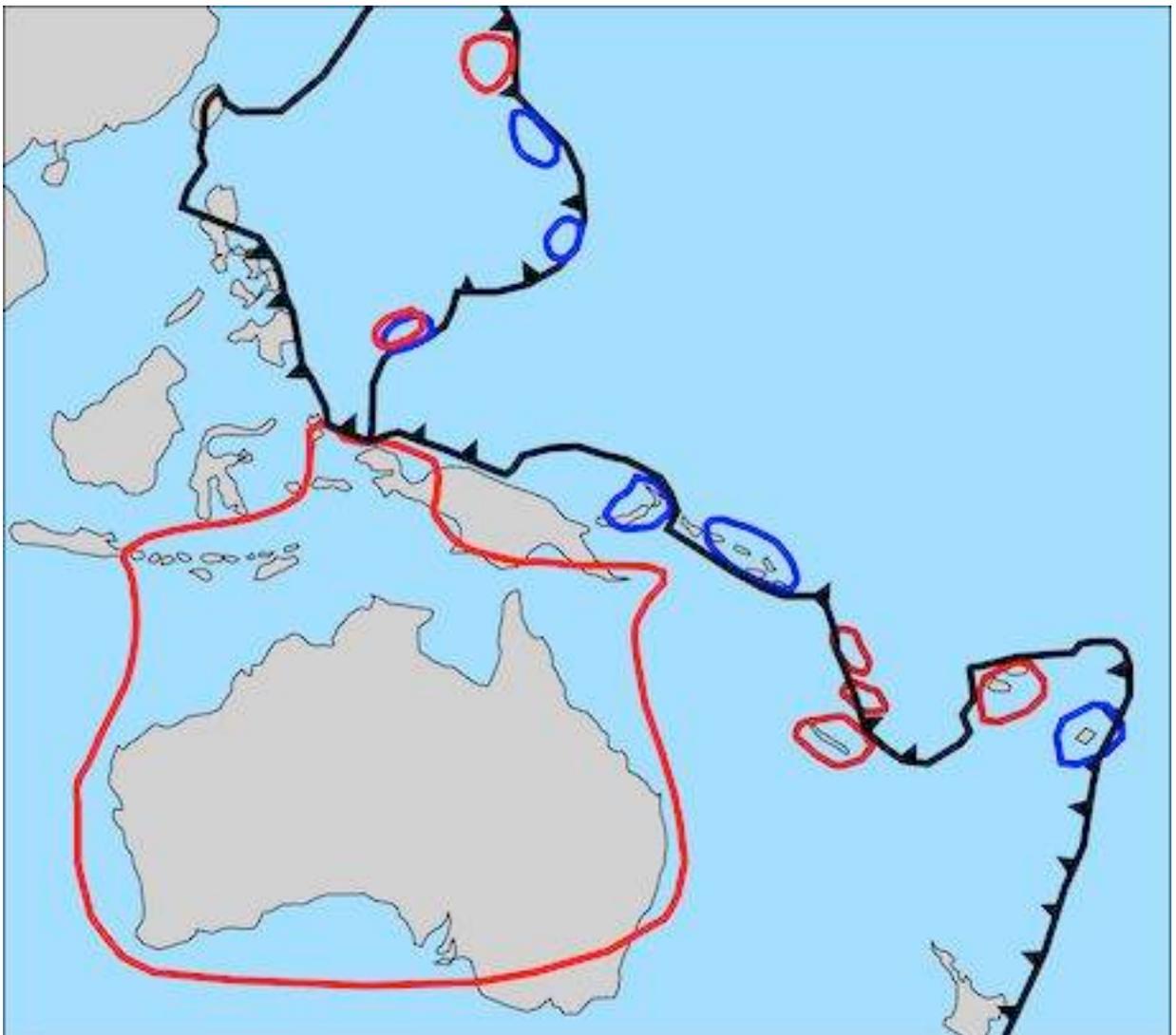


Fig. 6. Geographic relationship between the distributional boundary between the trans-Pacific lizard species *Cryptoblepharus poecilopleurus* (blue circles), and other western Pacific *Cryptoblepharus* species (red circles or outlines). Black lines – Pacific plate boundary (barbs are on the overriding plate).

The central Pacific group of flycatchers is not nested within the mainland clade as might be expected of a group dispersing out into the Pacific. Instead, the biogeographic and phylogenetic pattern of the flycatchers is consistent with a widespread ancestral range that included both continental (Australia/New Guinea) and oceanic island habitats. A vicariance history for the group involves, at the first division, two descendant distributions, one across the central and southwest Pacific, the other across eastern and northern Australia/New Guinea and Micronesia. This initial phylogenetic and geographic break for the sister taxa lies between Rennell Island (SW Solomon Islands) and the other Solomon Islands. The two localities (Fig. 8) are separated by a plate boundary, the South Solomon Islands Trench (marking a subduction zone), and the geographic distance between Rennell Islands and the other Solomon Islands was much greater in the past (Schuth *et al.* 2009, Seton *et al.* 2012, Holm *et al.* 2016). The phylogenetic relationships within *Dianella* are not fully resolved. However, the preliminary study by Muscat *et al.* (2019) suggests the existence of three allopatric groups within their ‘clade N’ that ranges between the eastern and western boundaries of the genus (Fig. 9).

The mid-Pacific boundary of the flycatchers at Hawaii – SE Polynesia is shared by numerous other taxa, including the *Tetraplasandra* group of Araliaceae (Heads 2012a: fig. 6-16), the plant genera *Meterosideros* (Heads 2012a, fig. 7.8) and *Santalum* (Heads 2012a: fig. 8-8), and the Pacific clade of Rutaceae (Heads 2012a: fig. 9-3). If this repeated pattern is not the result of 'chance', how might the biogeographic boundary be interpreted? A biogeographic clue is seen in the plant group *Bidens* sect. *Campylotheca* extending between Hawaii and Pitcairn islands (Fig. 10). This distribution shows the same eastern boundary as the other examples, while its sister group ranges across southern North America, Central America, the Caribbean, and northwestern South America. The phylogenetic break between these the two sister clades coincides with a divergent plate boundary (a spreading centre and mid-ocean ridge) termed the East Pacific Rise. This spatial relationship is consistent with a vicariance origin of the two clades, with an ancestral range in the Pacific being split apart by tectonic divergence at about 120 Ma (Heads 2012a). This vicariance origin is also applicable to many other taxa displaying differentiation at the same boundary. For example, the sister group of *Dianella* is the genus *Eccremis*, restricted to NW South America. The overall distribution can be derived from a widespread ancestor that straddled the Indian and Pacific Oceans. Tectonic displacement at the East Pacific Rise fragmented the ancestral range, causing the divergence of *Dianella* to the west, and *Eccremis* to the east (Fig. 11).

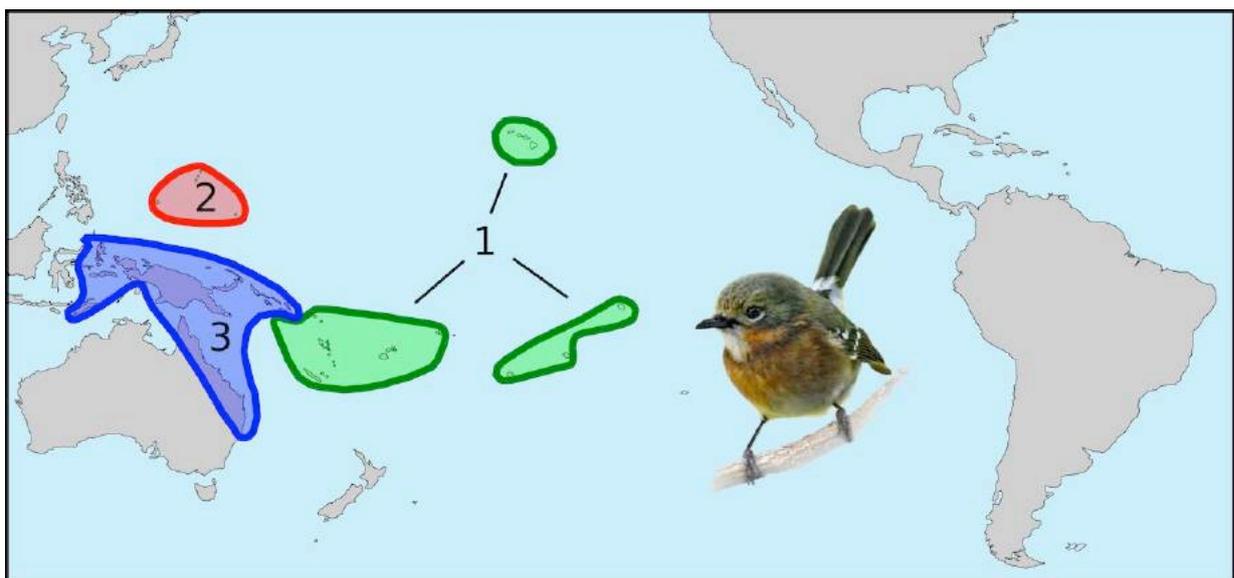


Fig. 7. Distribution of three sub-clades of Pacific fly catchers (*Monarcha* and allies; Monarchidae). Sub-clade 1 (*Chasiempis*, *Pomare*, *Mayrornis*, *Clytorhynchus* and *Neolalage*) is the sister group of subclades 2 (*Metabolus*, *Monarcha* p.p.) + 3 (*Monarcha* p.p.). Simplified from Filardi & Moyle (2005) and Heads (2012a: fig. 6-3).

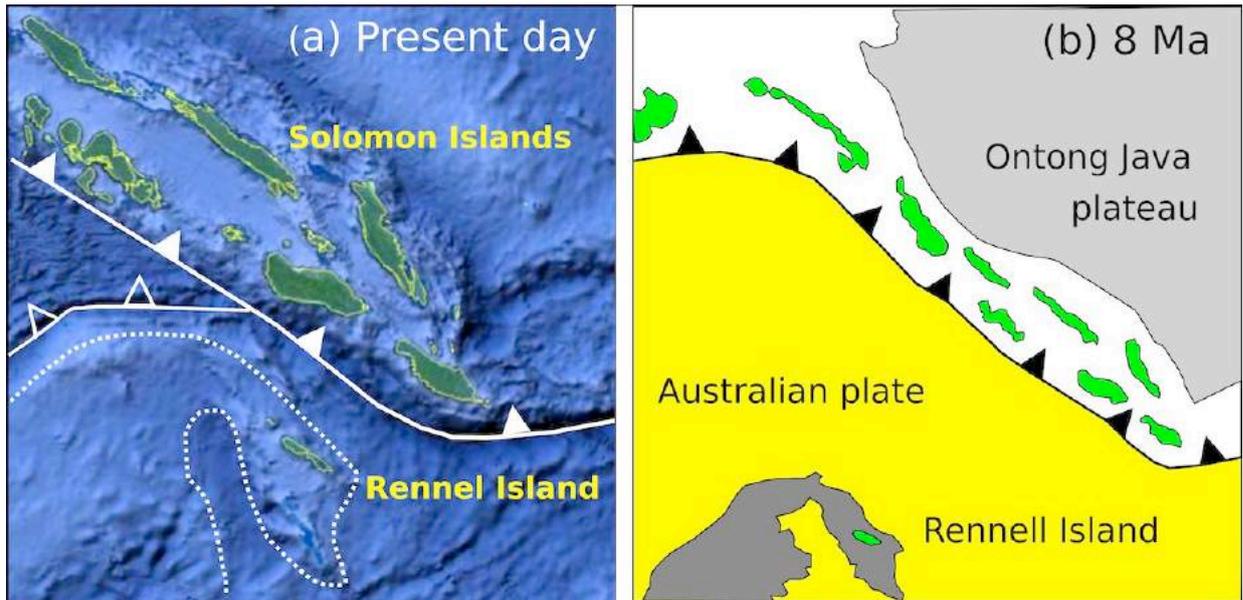


Fig. 8. Tectonic relationship of Rennell Island: (a) present day position on the Louisiade Plateau (dotted outline) south of the Solomon Islands subduction zone (with barbs on the overriding plate), (b) Reconstruction of Rennell Island and the main Solomon archipelago at 8 Ma (modified from Holm *et al.* 2016: fig. 6).

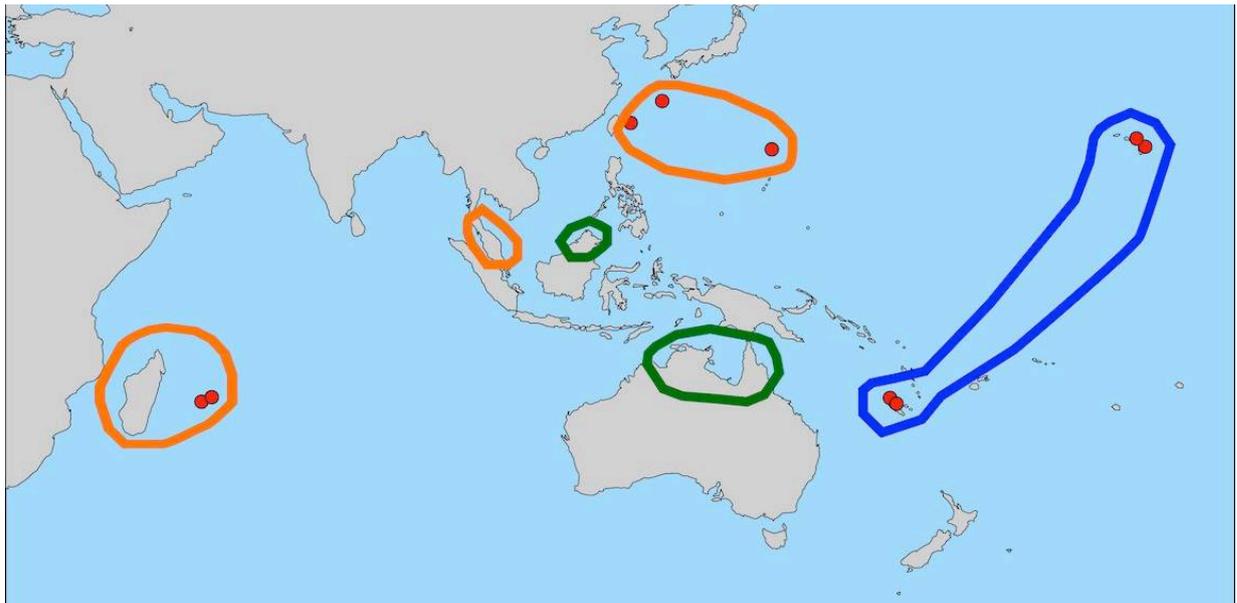


Fig. 9. Distribution of *Dianella* 'clade N' comprising three reciprocally allopatric monophyletic subgroups (orange, green, blue). (Based on a partial phylogenetic sampling by Muscat *et al.* 2019).

Lessons from biogeography and systematics

The examples discussed here illustrate how biogeography and systematics can go hand in hand in the analysis of biodiversity (Heads 2017a). Biodiversity is made up of biogeography and phylogeny. Spatial correlations between patterns of distribution and tectonics provide an empirical connection between geological history and biological history, just as Darwin (1859) predicted (see above). To paraphrase Gandhi, geography and phylogeny (biology) are together the left and right eyes of biodiversity. Without both of them, we cannot really see what is in front of us, let alone hope to preserve it.

An approach to biodiversity incorporating both systematics and geography allows novel assessments of biodiversity levels. It is generally recognized that the biodiversity of some areas is more prominent than that of others, and there have been various attempts to quantify such

differences by the areas' biological characteristics. These include numbers of species and higher-level taxa, as well as phylogenetic structure. However, without knowing the biogeography there is no biodiversity context to recognize the evolutionary significance of sister taxa. When geography is included along with systematics, it is possible to recognize biodiversity patterns that would otherwise be invisible. Unfortunately, most modern phylogenetic studies provide maps only of the *a priori* regions used for area analysis, and do not include range maps of the clades recovered.

The integration of biogeography and phylogeny to assess biodiversity can be illustrated by local endemics that have widespread, or even global sister groups. These local endemics may be small and obscure, but they have a high level of significance for biodiversity and its conservation (Heads 2017). For example, the angiosperm genus *Amborella* is the sister group to all other angiosperms, but it is found only in New Caledonia. The bird family Acanthisittidae is sister to all other passerines but is only known from New Zealand. These are examples of 'globally basal' endemics that combine local distribution with diverse, globally distributed sister groups, and so the areas they occupy can be accorded maximum values of biodiversity (Heads 2014 p. 184).

Crisp *et al.* (2011) considered the origin of *Amborella* to be “shrouded in mystery”. A non-mysterious vicariance explanation proposes a globally widespread angiosperm ancestor that initially diverged into two descendants, one of which was localized in the region now occupied by New Caledonia. The other descendant (the ancestor of all other angiosperms) was distributed over the rest of the world. This original allopatry was followed by range expansion of the larger clade overlapping with *Amborella* in the New Caledonia region (long before modern New Caledonia existed). Local endemics that are globally basal are concentrated in places such as New Caledonia, New Zealand, Madagascar and western Mexico, and indicate the great biodiversity of these regions and their importance for conservation.

In contrast with the methodology proposed here, the ‘ancestral area’ algorithms currently used (DEC, DIVA and others, as implemented in packages such as BioGeoBears; Matzke 2013) calculate centers of origin and routes of chance dispersal. However, these algorithms infer centers of origin and chance dispersal events where none may exist, as they calculate centers of origin in the regions of basal phylogenetic grades. These localities are just as likely to be the sites of original vicariance (Heads 2017a, 2019, Heads & Grehan 2021).

As for the timing of evolution, many readers may feel that the absence of old fossils proves that clade divergence dates calculated using biogeographic-tectonic calibration are wrong, and that molecular divergence dates, based on fossil calibrations, prove a more recent origin. These objections have already been addressed in great detail (Heads 2012a, 2012b, 2014, 2017a). To summarize: (1) fossils provide only the minimum age of taxa, and most species have no fossil record; (2) fossil-calibrated molecular divergence ages are minimum estimates only – they do not place any upper constraints on the potential age limits of taxa; (3) the widespread use of narrow priors in Bayesian analyses simply imposes the old belief that a clade's age can only be a little older than its oldest fossil.

Conclusions

Prevailing definitions of biodiversity as a purely biological assemblage of taxa fail to appreciate the combined geographic and systematic structure of biodiversity as a natural evolutionary pattern. The science of systematics can change this conceptualization by recognizing that the organization and composition of biodiversity comprises both geography and phylogeny. If systematics is to play a central role in documenting and interpreting biodiversity (not just its phylogeny) it will be necessary for systematists to recognize that the geographic patterns of phylogeny, in the form of mapped distributions, present the real world structure of biodiversity. Evolutionary biodiversity is phylogeny *and* biogeography, and the correlation of biodiversity with global tectonics is an empirical evolutionary reality.

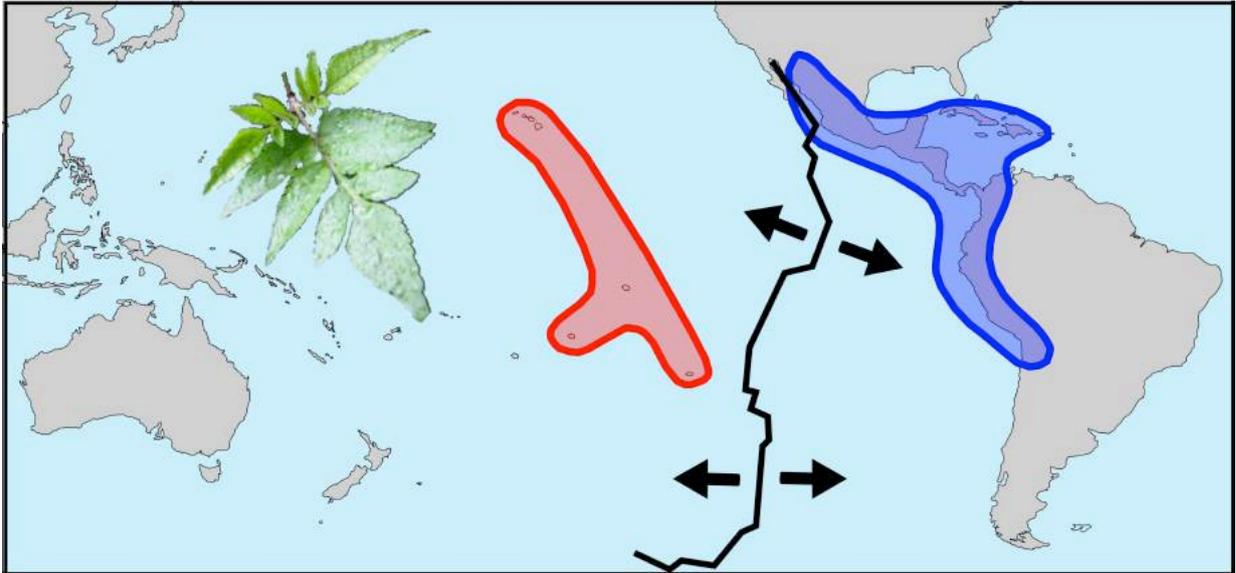


Fig. 10. Distribution of *Bidens* sect. *Campylotheca* (red) and its sister group sect. *Psilocarpaea* (blue). Black line – East Pacific Rise. Modified from Heads (2012a: fig. 7-6)

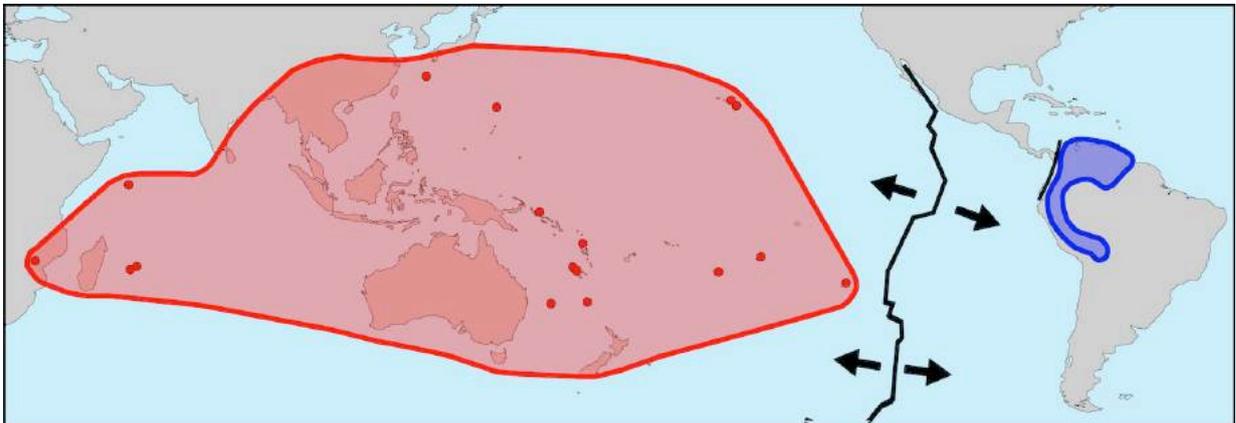


Fig. 11. Distribution of *Dianella* (red outline) and its sister group *Eccremis* (blue outline) either side of the East Pacific Rise (black line with arrows). Individual island localities of *Dianella* as circles. Black line along western edge of *Eccremis* – the Romeral fault zone. Distribution of *Eccremis* from Wurdack & Dorr (2009).

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