

Biogeography of Australasia

A Molecular Analysis

Over the last decade, molecular studies carried out on the Australasian biota have revealed a new world of organic structure that exists from submicroscopic to continental scale. Furthermore, in studies of global biogeography and evolution, DNA sequencing has shown that many large groups, such as flowering plants, passerine birds and squamates, have their basal components in this area.

Using examples ranging from kangaroos and platypuses to kiwis and birds of paradise, the book examines the patterns of distribution and evolution of Australasian biodiversity and explains them with reference to tectonic and climatic change in the region. The surprising results from molecular biogeography demonstrate that an understanding of evolution in Australasia is essential for understanding the development of modern life on Earth.

A milestone in the literature on this subject, this book will be a valuable source of reference for students and researchers in biogeography, biodiversity, ecology and conservation.

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Contents

	<i>Preface</i>	<i>page</i> ix
	<i>Acknowledgements</i>	xii
1	The spatial component of evolution	1
	Models of spatial evolution in biogeography	2
	Case-studies in and around Australasia	13
	Biogeography and dispersal	21
	Biogeography and genetics	26
	Biogeography and ecology	30
2	Evolution in time	32
	Equating the age of a node with the age of the oldest known fossil	32
	Using the age of islands or strata to date their endemic clades	44
	Using tectonics to date clades	53
	Mode of evolution: is evolution more or less clock-like?	57
	Case-studies in evolutionary chronology	62
3	Global affinities of Australasian groups	71
	Widespread Australasian groups with global sisters	71
	Australasian groups basal in panaustral complexes	72
	Australasia–Indian Ocean groups	73
	Australasia–Tethys affinities	81
	Australasia–Pacific groups	83
	Pacific + Tethys groups in Australasia	101
	Australasia–central Pacific groups	104
	Trans-tropical Pacific connections	106
	Distribution in a Pacific triangle: Australasia–western North America–southern South America	115
	Indian + Pacific Ocean groups	118
	Pacific + Atlantic groups	130
	Pacific + Indian + Atlantic groups	130
	Intercontinental affinities of Australasia: a summary	132

vi	Contents	
4	Biogeography of Australia	133
	Distribution in and around Australia	133
	Distribution within Australia: affinities between the coasts and the central deserts	135
	The south-western Australian biota	143
	North-western Australia	151
	The Great Dividing Range	163
	Tasmania	165
	McPherson–Macleay Overlap	167
	The Cairns region in north-eastern Queensland	176
	Breaks around Torres Strait and the Coral Sea	177
5	The Tasman–Coral Sea region: a centre of high biodiversity	181
	The Tasman–Coral sea region as a centre of biodiversity	182
	Globally basal endemics in the Tasman–Coral sea region	188
	Interpretation of the Tasman–Coral centre	195
	The ecological context of the basal Tasman groups: arapod forests	200
6	Distribution in and around the Tasman region	204
	Tectonic context of the Tasman region and the evolution of island biotas there	204
	Distribution within the Tasman region	211
	Australia–New Zealand connections	212
	New Zealand–New Guinea connections	218
	Groups centred on the Tasman and Coral seas	230
	Phylogenetic breaks around New Caledonia	235
	A case-study: Ericaceae in the Tasman region	238
7	Biogeography of New Zealand	246
	New Zealand geology	246
	North-eastern New Zealand	247
	Southern New Zealand: Campbell Plateau and the New Zealand subantarctic islands	253
	The Alpine fault: disjunctions and other breaks at a plate boundary	255
8	Biogeography of New Caledonia	261
	Absences in the New Caledonian biota	262
	Biogeographic affinities of the New Caledonian biota	263
	A case-study: the New Caledonian palms and their relatives	275
	New Caledonian terranes and tectonic history	282
	Areas of endemism in New Caledonia	292

	Contents	vii
	Terrane tectonics and biogeography in New Caledonia	305
	Towards a new model of New Caledonian biogeography	310
9	Biogeography of New Guinea and neighbouring islands	313
	Biogeography of the New Guinea region	313
	New Guinea as a global centre of differentiation in several bird groups	317
	Biogeographic differentiation in mainland New Guinea	327
	The Bismarck Archipelago and the Solomon Islands	342
	Vanuatu and Fiji	346
	West of New Guinea: the Maluku Islands (the Moluccas) and Sulawesi	350
10	Biogeography of the Philippines	356
	The traditional model of Philippines biogeography	358
	Geology of the Philippines	360
	The accreted arc/metapopulation model of Philippines biogeography	363
	Philippines groups with widespread sister-groups	364
	Philippines connections with areas further east	377
	Distribution within the Philippines	389
	Appendix: eastern and western Philippines tracks	399
11	Conclusions	402
	Evolution and space	402
	Evolution and time	403
	Panbiogeography, tectonics and evolution	404
	Darwinian and neo-darwinian models of evolution and ecology	404
	Beyond the CODA model of evolution and ecology	406
	<i>Abbreviations and terms</i>	408
	<i>Glossary</i>	409
	<i>References</i>	411
	<i>Index</i>	484

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Preface

The theme of this book is the distribution of plants and animals in Australasia, the region made up of Australia and the larger islands that fringe its east coast – New Zealand, New Caledonia and New Guinea. Geographical information on particular clades (taxonomic groups) has been collated for this book from molecular studies carried out over the past decade or so. The molecular revolution has revealed a whole new world of beautiful, intricate structure in nature, just as the microscope and the telescope did four centuries ago. Sequencing studies are providing a fabulous new wealth of data on geographical distribution in all kinds of organisms and from an intercontinental scale down to a local level.

Ever since the region was discovered by the outside world, biologists have had a special interest in the flora and fauna of Australasia. The habitats range from subantarctic islands to alpine peaks, deserts, hot, humid forests and coral reefs, and Australasia has some of the most unusual plants and animals in the world. These give a different perspective on the ‘normal’ groups found in most places. For example, the New Caledonian plant *Amborella* is the sister-group of all other flowering plants, the New Zealand tuatara is the sister of all the lizards and snakes, and the New Zealand wrens (*Acanthisittidae*) are the sisters of all other perching birds. Many other groups show similar patterns and this book examines possible explanations for this.

Most of the studies discussed here are based on molecular evidence, as it allows such great phylogenetic and biogeographic resolution. On the other hand, traditional taxonomic revisions based on morphology often examine larger samples and suggest relationships for even the rarest and most inaccessible populations. Morphological studies can shed light on detailed aspects of distribution and are cited below for some areas or groups in which molecular surveys have not yet been carried out.

The work discussed here has been published in exemplary accounts based on well-conceived surveys, using the latest techniques. Nevertheless, there are often geographical or phylogenetic gaps in the sampling, the resolution of the phylogenies is sometimes incomplete and statistical support for the clades varies. Other important aspects of the studies include the parts of the genome sequenced, the methods used to establish sequences and the methods used to construct a phylogeny from the sequence data. Information on all of these is available in the original papers and the details are not referred to here. Instead, the focus is on the results – the geographical patterns – that have been obtained so far.

The phylogenies represent interim hypotheses and will change, to some extent, with further work. But although the situation is still fluid, in many groups the phylogenies are stabilizing in a remarkable way and well-supported clades with coherent distributions are emerging. How can this intriguing new information best be put to use? Can it help answer the many unresolved questions about evolution and ecology?

This book describes and illustrates some of the main distribution patterns involving Australasia and also explores ideas on their historical development. Although fascinating new phylogenies are now appearing almost daily, the interpretation of the distributions is lagging far behind the descriptive studies; authors still seem more concerned with producing new results than explaining them. Most of the interpretations that are being offered are based on old concepts inherited from the Modern Synthesis or on minor variations of these.

Instead of relying on these approaches, the method of interpretation adopted here is that of panbiogeography, a synthesis of plant geography, animal geography and geology (Craw *et al.*, 1999; Heads, 2012a). This method dissects the geographic patterns of molecular groupings, compares them with patterns in other groups, and synthesizes the results with current ideas on Earth history. Mapping is fundamental in this process. In geology, maps have been an integral part of the discipline since its origin and a mapping project is a standard component of first-year university courses. It is impossible to imagine a regional geological study without maps. Yet distribution maps did not become the norm in biological studies of groups, floras and faunas until the 1960s; even now, many taxonomic monographs are published without any distribution maps at all. The situation is changing, though, and biologists are taking a much more active interest in distribution. This is because molecular studies have found so much impressive, unexpected geographic structure in most groups. In many cases the molecular groupings show a much closer relationship with geography than with morphology, or at least with traditional interpretations of morphology. Increasing numbers of papers in molecular phylogenetics are including distribution maps, as the clear-cut patterns are among their most interesting results.

The distribution patterns are compared here with the underlying tectonic developments in Earth's history and with the fossil record. The fossil record is useful for dating, but most groups have no fossils and even in groups with many fossils, these can only give minimum ages for clades – the actual age can be much older. Panbiogeography estimates the actual ages of groups by relating distributions with spatially associated tectonic and climatic events, such as the last, great rises in sea level in the Cretaceous period. Many authors are now abandoning the fossil record as a source of maximum clade ages and are instead calibrating phylogenies with single tectonic events. Panbiogeography extends this approach by employing multiple tectonic correlations to calibrate many nodes on a phylogeny. This approach involves a broad engagement of biogeography and tectonics.

The results in the proposed model are unexpected, as the groups are inferred to be much older and long-distance dispersal much less significant than has been thought. Yet the new model offers distinct advantages, as it does not rely on chance events to explain distribution patterns and instead provides a coherent synthesis of phylogeny and Earth history. If distributions were the result of chance dispersal, each group would

have a different, idiosyncratic pattern and there would be little overall structure within or among groups. Instead, most distributions are shared by many unrelated plants and animals that often differ in their ecology and means of dispersal. This suggests that the repeated phenomena are probably the result of general causes, such as geological or climatic change. As the geographic patterns continue to be investigated with molecular work they are becoming clearer and, in addition, the same distributions and breaks are recurring in different groups. As these results accumulate, chance dispersal appears less and less likely to be a general explanation for biogeography.

The relationship between biogeography and ecology has often been problematic, but there are hopeful signs of a new integration of the two fields. Ricklefs and Jenkins (2011) wrote: ‘The schism between ecology and biogeography possibly peaked during the 1970s, soon after Robert MacArthur (1965, 1972) explicitly excluded history from the purview of ecology . . . one could argue that ecologists further weakened the study of biogeography through the development of the equilibrium theory of island biogeography, which was essentially nonhistorical . . . Only after the general acceptance of plate tectonics in the 1960s and the development of increasingly analytical approaches to studying geographical distributions, such as panbiogeography (Croizat, 1958), vicariance biogeography (Wiley, 1988), analytical biogeography (Myers and Giller, 1988) and areography (Rapoport, 1982), did biogeography experience a resurgence that eventually commanded the attention of ecologists . . .’.

If a group’s distribution represents inherited information, this can shed light on the group’s ecology and its evolution. This book discusses many of the interactions among tectonics, biogeography and ecology; two of the main processes are passive uplift of populations during orogeny and stranding of coastal groups inland following retreat of marine incursions.

No two groups have identical distributions, but many share similar, distinctive features, including their main phylogenetic and geographic breaks or nodes. The location of these nodes in Australasia, their relationships with other nodes and their development in space and time are the main topics explored in this book.

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