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Introduction: islands and plants

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The complexity of the modern way of life has meant that humankind is not simply one member of a natural ecosystem but is a user, consumer, dominator and potential destroyer of all the Earth's ecosystems. Unfortunately nowhere is this more apparent than in the fragile ecosystems of the world's oceanic islands.

Recent estimates of the number of flowering plant species on the world's islands suggest that of the 50 000 or so insular endemics, some 20 000 are threatened with extinction. The same is true for other island organisms, and Johnson and Stattersfield (1990) estimate that the extinction rate among island birds in historical times is about 40 times greater than in continental species.

On the other hand, the consensus among biologists is that island studies contribute important ideas, theories, models and tests into mainstream biology (Whittaker, 1998) and island ecosystems are now considered environments in which to seek answers to complex questions about the patterns and pathways of evolution. The possible loss of 40% of these unique plant species, many of them still known only in an alpha-taxonomic state (Bramwell, 2006) is, therefore, a source of concern. Even though there has been considerable progress in its study, the challenge of understanding 'island biology' remains but it is, itself, now threatened by the probability of ever rising extinction rates accelerated by new factors such as global change, in particular the disruption of previously stable climates.

Some recent publications on island biology

Major developments in island biogeography have taken place, however, over the past 30 years or so and are characterised by the application of new concepts and techniques in molecular systematics as well as more profound studies of reproductive

The Biology of Island Floras, eds. David Bramwell and Juli Caujapé-Castells. Published by Cambridge University Press.

biology and of the role of hybridisation in insular speciation. We should, perhaps, describe these developments as 'helping to explain Darwin' by using modern methods to elaborate and expound the mechanisms, pathways and results of evolution by natural selection on islands.

During this period, a significant number of new publications have appeared, each, in its own right, making a significant contribution to island biology. Among the most important are those written or edited by Williamson (1981), Grant (1998), Whittaker (1998) and Stuessy and Ono (1998). Williamson takes what he refers to as a modern look at McArthur and Wilson's Theory of Island Biology and especially its strengths and weaknesses in relation to species numbers on islands. He concludes, after an extensive review of published data, that the hypothesis of immigration and extinction being in balance is generally correct. It is, however, perhaps not as dynamic a process as envisaged by the original authors, as many immigrants do not establish as long-term colonisers and so the equilibrium requires rather more arrivals than extinctions for species numbers to remain stable. Williamson also considers island ecosystems and is emphatic about the need to relate the structure of island communities and their ecological processes to the evolutionary processes, which form the distinct island biota.

Grant, in 1998, compiled and published an indispensable volume under the title *Evolution on Islands*. In this book, he poses the two fundamental questions in evolutionary biology – 'how does evolution occur?' and 'why does evolution occur?' – and he emphasises the contribution in answering these questions of modern studies of what he terms 'evolution in the relative simplicity of island environments'. In this respect Barratt (1998), in the same volume, considers that many of the problems of evolutionary biology can be studied by using island plants as model systems for investigating the genetic basis of adaptation and speciation. He warns, however, that as islands vary considerably in area, altitude, climate and isolation, broad generalisations about insular evolution may not always apply.

The phylogeny of island plants, a controversial subject over the past 30 years, is also considered and Grant himself comments on the need to reconsider some rather neglected factors such as introgression and hybridisation on speciation and, indeed, on the reconstruction of phylogenies. Thorpe and Malhotra (1998) in their chapter also emphasise the need for caution in phylogenetic interpretation, noting that 'adaptation to current ecological conditions appears to be a primary force influencing morphological population differentiation irrespective of phylogenetic history'. In a further chapter, Clarke *et al.* (1998) reinforce Grant's views on hybridisation and introduce the concept of 'molecular leakage' to explain the genetic similarity between species with widely diverse morphology and ecology. They consider that the results of even very low rates of hybridisation or introgression in some insular organisms can be 'misleading in the interpretation of phylogenetic history'.

Whittaker (1998), in his synthesis of recent developments in the subject, presents an excellent general survey of island biogeography up to the end of the pre-molecular age, though with a considerable emphasis on fauna. On the other hand he devotes only a single page to phylogenetic systematics and cladistic biogeography, and the major contribution made to modern biogeographical concepts by Leon Croizat (1958, 1964), whose alternative ideas of space, time and form and his attempts at re-evaluation of Darwinian interpretation do not even warrant a mention. Cladistic biogeography and its more recent offshoot phylogeography are currently, however, important tools in the interpretation of molecular data.

Apart from the above general texts, several more specifically regional books have appeared. These include Stuessy and Ono (1998) *Evolution and Speciation of Island Plants*, which places a strong emphasis on the Pacific Ocean islands. Wagner and Funk (1995) and Ziegler (2002) both treat distinct aspects of biogeography, ecology and evolution in the Hawaiian archipelago. In addition to these, a number of original ideas on island biology have been presented in individual scientific papers and, among these, Silvertown (2004), for example, has offered a very plausible hypothesis of the role of competitive exclusion and 'niche pre-emption' to explain the inability of new colonisers to establish on many islands despite frequent dispersal events from continental sources. Vargas (2007) has also developed an interesting hypothesis for the interpretation of Macaronesian phytogeography (see below) which may also be applicable to many other island situations throughout the world.

The biology of island plants

During the past 30 years, the renewed interest in island plants in the light of new data from molecular biology has resulted in the formulation of various new concepts. These are reviewed and discussed in the chapters in this book and are briefly summarised below.

Concepts

In Chapter 2, Daniel Crawford *et al.*, building on the earlier contributions of Carlquist (1974) and Ehrendorfer (1979), present a new overview of the diversity of reproductive biology systems in insular lineages and emphasise the need for future research to integrate traditional studies with new approaches such as the use of molecular markers to estimate outcrossing rates. They specifically compare reproductive biology, including a review of mating systems, in different island groups and attempt to explain similarities and differences. The post-colonisation changes in the reproductive biology of insular plants compared with their nearest continental relatives are also considered and the authors emphasise the importance of reproductive biology for conservation and the need to include conservation implications in its study.

In Chapter 3, Paula Posadas *et al*. consider the need to combine molecular phylogenetics with an innovative spatial methodology involving historical biogeographic approaches such as panbiogeography and track compatibility analysis as well as analysis of parsimony and biota similarity to explain patterns of distribution and to formulate testable biogeographical hypotheses.

Modern studies of island diversity

In the field of insular diversity, Sterling Keeley and Vicky Funk (Chapter 4) take a new look at the origin and evolution of the flora of the Hawaiian archipelago. By comparing pre-molecular age studies carried out by Carlquist (1965, 1974) and Wagner and Funk (1995) with molecular data, they re-evaluate the biogeographic affinities of the flora including probable areas of origin, dispersal modes, age of dispersal and probable number of colonisation events for most of the major groups of Hawaiian endemics. The molecular data provide considerable insight into the direction and timing of colonisations, patterns of adaptive radiation in the archipelago and the role of hybridisation in the evolution of Hawaiian endemics.

The Galapagos Islands have been, since Darwin drew the world's attention to them in the nineteenth century, at the forefront of island biology. In Chapter 5, Alan Tye and Javier Francisco-Ortega review and revise current ideas on the origin and evolution of their unique flora in the light of both molecular studies and recent research using traditional methods. They consider how new information affects conclusions on source areas and colonisation dates and indicates the former existence of now submerged islands. Evolutionary processes within the archipelago are also examined and the role of human activity in altering the flora addressed. In conclusion, the authors make a number of recommendations for the direction of future research.

Michael Maunder *et al*., in Chapter 6, emphasise the importance of the Caribbean islands as biodiversity centres or 'hotspots' and review the taxonomic and ecological diversity of the region. They also consider the phylogenetics and phytogeography of a number of endemic genera and present a new review of Caribbean conservation issues and challenges.

Madagascar has been one of the islands of special attention during the past 30 years. As John Dransfield and Mijoro Rakotoarinivo demonstrate in Chapter 7, the palm flora, for example, is an astonishing one with 174 described species in 14 genera and with many more still to be documented. The authors comment on the remarkable diversity of relationships of the Madagascar palms with their nearest relatives in regions as close as South West Asia and Africa or as far away as Australia, Indo-China, New Guinea and even South America. They also discuss the diversity of palm ecology on the island and its implications for conservation.

Lisa Banfield *et al.* in Chapter 8 consider the phytogeography of the fascinating island of Socotra in the light of both the classical view of the origins of the flora and more recent molecular studies. Earlier studies suggest that the island acted as a refuge for relictual vicariants, but recent molecular work indicates that later long-distance dispersal played a role in colonisation and establishment of Socotra's flora. The authors consider both aspects in a detailed critique and defend the relictual hypothesis for various taxa. In their conclusions, they include comments on the likely effects of climate change on the conservation of the flora.

One of the least known insular floras is that of New Caledonia with about 75% endemism and a large number of ancient, relict lineages including gymnosperms and basal angiosperm groups. On the other hand, geological evidence of submergence of the island in the Eocene is difficult to reconcile with a relict Gondwana hypothesis for the origin of the flora. In Chapter 9 David Bramwell suggests that there is, indeed, a Gondwana element in the flora but at the same time there are some derived groups of more recent arrival and that both have undergone radiation and diversification on the island. He also comments on the current state of the island's unique vegetation types and human influence on them, suggesting that many plant species on New Caledonia are under threat and formal assessment of their conservation status should be completed.

In Chapter 10, a study of one of the world's most inaccessible island groups, the Pitcairn Islands (Pitcairn, Henderson, Oeno and Ducie), Steve Waldren and Naomi Kingston analyse the biogeographical affinities of the flora and evaluate the endemic taxa and their origins including molecular studies of the largest genus, *Peperomia*. They conclude that insular endemics have originated through geographical isolation rather than by radiation.

Brian Murray and Peter de Lange, in Chapter 11, also consider the biogeography of a Southern Hemisphere insular flora, that of New Zealand. They do it, however, from a more classical approach based on chromosome analysis, especially of the ancient gymnosperms of the islands. Molecular evidence suggests a rather recent origin for many of the endemic angiosperms and their evolution is evaluated using data on polyploidy, aneuploidy and interspecific hybridisation.

The Macaronesian model

The Macaronesian region has been a major focal point for the molecular study of island floras and four chapters here summarise the 'Macaronesian model' for molecular systematics. Chapter 12 by Juli Caujapé-Castells provides a broad overview of the wealth of data generated over the past two decades and their impact on the present understanding of the region's flora. At the same time, he highlights some deficiencies and gaps in the data, which indicate as many new problems as questions answered, and suggests fields for future research. He emphasises the need for testable biogeographic hypotheses. In this context, of recent published works on the region, the paper by Vargas (2007) is an important one from a molecular phylogenetic point of view. In an excellent summary of the evolutionary history of Macaronesian plants, Vargas revives the ideas presented in their day by authors such as Sunding (1979) and Bramwell (1972, 1976, 1985) on the relict nature of the insular floras. He introduces the concept of lineage relictualism (ancient lineages) in terms of absolute time to describe those groups originally colonising Macaronesia before the start of the Quaternary period. His views are supported by Francisco Ortega *et al.* (1997) who suggest, based on molecular evidence, that the exclusively Macaronesian genus *Argyranthemum* of the subtribe Chrysantheminae 'is old relative to continental genera of the subtribe' and is sister to other modern Mediterranean members of the tribe. Estimating divergence times using a molecular clock, these authors indicate that *Argyranthemum* diverged from the rest of the Chrysantheminae, possibly from a now-extinct common ancestor, between 2.5 and 3 million years ago (Ma), i.e. in the Tertiary period. They conclude that the results of three independent sets of molecular data are consistent with a previous hypothesis that some members of the Macaronesian flora may be ancient in relation to their continental relatives. Vargas (2007), reviewing 34 molecular phylogenies and molecular clocks of Macaronesian plant groups, suggests that the majority of these may be considered as lineage relicts with their origin in the Mediterranean region during the Tertiary period. On the other hand, some scepticism remains about the value of molecular clocks in general and, in particular, in situations of rapid radiation. Thomas *et al.* (2006), on the basis of observations that substitution rates vary widely between lineages, question the existence of a universal molecular clock, suggesting that the results of extrapolation from one situation to others should be treated with caution.

Dolores Lledo *et al.* in Chapter 13 consider the biogeographical relationships between Macaronesian endemics and their Mediterranean relatives. The relationships between continental and insular groups, however, still remain partially unresolved. In the case of *Limonium* several colonisation events are postulated and *L. dendroides* is considered to be an isolated relict taxon. The principal group in the Canary Islands, subgenus *Pteroclados* appears to be monophyletic, the result of a single colonisation which probably took place about 7 million years ago and may be considered to be an ancient lineage (Vargas, 2007).

Alain Vanderpoorten *et al.* in Chapter 14 present a review of recent research on the under-studied cryptogam flora of the Macaronesian region. They look at patterns of endemicity and phylogenetic relationships and suggest that the differences in patterns of diversity and relationships between the angiosperm and cryptogam floras may be indicative of very different evolutionary processes. Finally, possible explanations for observed differences are considered and compared, shedding new light on the evolution of insular diversity.

Ecology and conservation of island floras

One of the principal conservation problems facing island plants is competition from invasive alien species. Generally, due to the influence of humans, almost all islands have been colonised by introduced species, often displacing their natural vegetation and competing for niches with individual endemic species. Michael Kiehn, in Chapter 15 on invasive, non-native species, outlines a number of examples and reviews the possible strategies and measures to be taken for native flora conservation and the eradication of aliens.

Ole Hamann, in Chapter 16 on conservation needs in the Galapagos Islands, presents a review of the ecology and demography of the native flora particularly in relation to volcanic eruptions and extreme climate events such as El Niño. He describes a singular example of the negative influence of humankind on one of the scientifically most important archipelagos and outlines the measures needed to restore and protect the flora.

Madagascar is the fourth largest island in the world and has between 10 000 and 12 000 species of plants, of which some 90% are endemic. Unfortunately human settlement of the island almost 2000 years ago has caused enormous destruction and over 80% of the original forest has been cleared. Recent developments outlined by Stuart Cable in Chapter 17 on conservation, however, permit a degree of optimism for the future of the Madagascan flora with the creation of new protected areas through 'debt for nature' exchanges and the involvement of local communities in conservation.

David Bramwell in Chapter 18 gives an account of some of the future problems for island biodiversity. He considers the potential effects of climate change on insular floras, especially in relation to the particular conditions found in island communities. Almost 35 years ago, Sherwin Carlquist, in his book *Island Biology* (Carlquist, 1974) defined a series of characteristics common to many organisms from islands throughout the world as the 'island syndrome'. This syndrome includes such phenomena as woodiness and longevity in generally herbaceous groups of plants and gigantism in animals, reduction of dispersal capacity through enlarged seeds, diminished efficiency of dispersal mechanisms such as a depauperate pappus in plants and the loss of flight capacity in birds and insects. The characteristics of the 'island syndrome' do not seem to aid either adaptation or migration. Insular woodiness and the tendency towards longevity, implying longer generation times, is not conducive to rapid adaptation to changing climatic and ecological conditions. In general terms, therefore, it can be said that the island syndrome creates a critical balance between insular endemics and their environment that can easily be disrupted by climate change and does not help the prospects for their *in situ* conservation in the face of the rapidly changing conditions brought on by climate change.

Jennifer Trusty *et al.* (Chapter 19) consider all the native species including 36 endemics to be threatened with extinction due to the degradation of habitat on the Costa Rican island of Isla del Coco. Applying the minimum area requirements of the IUCN Red List criteria they found, however, that all the species should be included in the CR (critically endangered) category even though they have widely different population sizes and habitat availability. They sensibly suggest that population size should be given priority over area occupied on small oceanic islands. In their contribution, the authors also examine all the threats to Isla de Coco species and make recommendations for their conservation.

Sara Oldfield in Chapter 20 revises the situation of various insular floras and provides a number of examples of their vulnerability to pressures from tourism and development, exotic predators and competitor species. She indicates the need for future conservation planning to take into account a new factor, global climate change. As a possible response to the requirements, she emphasises the need for additional measures to support *in situ* conservation and outlines the future role for botanic gardens and seed banks in securely storing wild plant material on a long-term basis and making it available for conservation projects.

In Chapter 21, a final summing up of the contributions to the book, Vernon Heywood notes that more than just climate change is affecting insular floras and considers this to be one more, very important, factor in the series of problems they face. He emphasises the enormous quantity and quality of biological diversity still surviving on the world's islands but considers the future of island biodiversity to be very hazardous indeed.

Epilogue on island floras

Ever-expanding agricultural areas, urbanisation and other types of human land use surround protected natural areas. They, therefore, are becoming ever more isolated from each other, creating islands of biodiversity in an 'ocean' of habitat destruction and restriction of gene flow. Eventually such isolation will mean that individual protected areas will be subject to the principles of island biogeography and insular evolutionary processes. Therefore, our knowledge of island biology will become increasingly important in the management of conserved areas, especially in the face of the increasing ecological pressures resulting from climate change, which may well alter both the rates of evolution and extinction in protected areas not only on islands but in general.

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