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Journal

Frontiers of Biogeography, 7(1)

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Publication Date

2015

DOI

10.21425/F5FBG24493

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perspective

A new golden era in island biogeography

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Abstract. For two centuries, islands have served as rich sources of inspiration and data for biogeographers, thus gaining renown as ideal natural laboratories. Their research potential continues to expand today thanks to the combined application of recent advances in several scientific fields. First, increasingly detailed geological and palaeoecological data are extending our understanding of the history of development of island biotas. At the same time, rapid methodological advances in molecular evolutionary biology and systematics are revealing the pathways by which species colonized islands, evolved, and formed communities. Third, basic data on species distributions are being collected from increasing numbers of islands and taxa, distributed widely through electronic resources, and analyzed with powerful software to reveal macroecological patterns. The pace and quality of recent advances signal a promising future in which islands will continue to play key roles in revealing how biodiversity is produced and maintained.

Keywords. Archipelago, biology, ecology, endemic, evolution, geology, methods, phylogeny, species, taxonomy

Introduction

Since the time of Charles Darwin and Alfred Russel Wallace, among others, islands have played a prime role in the development of biogeography. The Equilibrium Theory of Island Biogeography (McArthur and Wilson 1963, 1967) is by far the most widely cited theory in the field. Many key biogeographical concepts—including long-distance dispersal, species-area relationships, assembly rules, speciation, natural and anthropogenic extinctions, and biological invasions—have been formulated, further developed, or tested through island research (Warren et al. 2015). However, since the 1960s and 1970s, when many of these ideas were developed and the major theoretical frameworks of modern biogeography were outlined—again, often based on island research (Elton 1958, Wilson 1961, Mayr 1963, MacArthur and Wilson 1963, 1967, Simberloff 1970, Carlquist 1974, Diamond 1975, Lack 1976)—a dis-

proportionate amount of island biogeography research has centred on repetitive tests of the validity and generality of the Equilibrium Theory of Island Biogeography across different island groups and taxa. In this perspective article, which is inspired by the quantity and quality of scientific work presented at Island Biology 2014¹ (an international conference, held in Honolulu, Hawaii, 7–11 July 2014), we propose that the field is now entering a new golden era. We suggest that three major developments that have risen to prominence over the last two decades are presently nurturing a phase of innovation and progress in island biogeography. First, through new information from the geosciences, phylogenetics, and palaeoecology we are gaining an increasingly richer and more realistic understanding of the geological and biological development of islands and their biotas. Second, we are experiencing a rapid expansion of the comprehensiveness of data avail-

¹ Abstracts of all communications are available at <https://sites.google.com/a/hawaii.edu/islandbiology2014/home/scientific-program>, last accessed 2/3/2015

able to island biogeography, covering many more taxonomic groups and islands. And third, new theoretical and methodological advances—including through the rapidly growing field of macroecology—are helping island biologists to discern increasingly sophisticated patterns in the abundance, distribution, and diversity of island biota over large spatial scales.

Toward a richer understanding of the geological and biological development of islands and their biotas

Geosciences

New findings from the geosciences are helping us to better understand the highly dynamic ontogeny of islands and are also revealing the changing connectivity both between continents and islands, and between islands themselves. Multi-beam scans of the ocean floor are yielding new, increasingly complete and accurate, and sometimes surprising bathymetric charts of archipelagos and the waters surrounding them, revealing extraordinary numbers of seamounts and guyots (former islands now drowned) both within archipelagos and between archipelagos and continents. Such data enhance our ability to analyze the effects that sea level regressions and transgressions related to the glaciation cycles have had on the connectivity between continents and islands (Warren et al. 2010, Ali and Aitchison 2014).

Bathymetric maps also enrich our understanding of the dynamism of island area, topography (including maximal elevation), and land bridges within archipelagos during glaciation cycles (e.g., Price 2004, Warren et al. 2010, Fernández-Palacios et al. 2011, 2014, Rijdsdijk et al. 2014). Glacial cycles have caused island sizes to fluctuate, and many now-separated islands were connected when sea level was lower. Furthermore, the recent discovery on the ocean floors of the collapsed remains of catastrophic landslides that destroyed significant parts of islands (e.g., Coombs et al. 2004), and evidence of the effects of the resulting tsunamis on nearby islands, together with the reappraisal of the role of glaciation cycles and their associated sea level oscillations, have helped the progressive shift from an

equilibrium towards a disequilibrium paradigm in island biology (Heaney 2000, Heaney et al. 2013).

The methodological revolution in dating island rocks has similarly emphasized disequilibrium dynamics, providing increasingly accurate and precise maximum and minimum geologic ages of emerged and drowned islands (Price and Clague 2002, Fernández-Palacios et al. 2011). Such accurate dating has enabled the measurement of small-scale ecological processes (colonization, ecological fitting, etc.), as well as the construction of reliable molecular clocks, by which crucial biological events (dispersal, diversification, adaptation, vicariance, extinction, etc.) can be better related to geological events that have shaped the history of a specific island or archipelago.

Finally, historical climatology reconstructs changing wind patterns and sea currents over time, which can help explain surprising biogeographic connections between distant islands—possibly including how Polynesians reached Easter Island and New Zealand (Goodwin et al. 2014).

Phylogenetics

Since phylogenetic studies were first developed, these methods have been used to elucidate evolutionary relationships among selected island taxa. Today, in the best-studied archipelagos, there are increasingly detailed phylogenies for entire taxonomic groups, such as Hawaiian silversword alliance (Carlquist et al. 2003) or floras such as in Macaronesia (Caujapé-Castells 2013). Such comprehensive phylogenetic datasets are being used to test biogeographical, ecological, and evolutionary hypotheses such as the importance of monophyly vs. polyphyly in shaping endemic taxa; cladogenesis vs. anagenesis in insular biotas; adaptive vs. non-adaptive speciation, or empty niches in explaining radiation—or the lack thereof—on islands (Silvertown 2004, Herben et al. 2005, Silvertown et al. 2005).

A recent paradigm shift in island biogeography, triggered through phylogenetic research, is the revelation of retro-colonizations (Hutsemékers et al. 2011, Siqueira 2012) or boomerang events *sensu* Caujapé-Castells (2013) from islands to continents, thus refuting the wide-

spread idea that islands are evolutionary dead ends (Carine et al. 2004, Bellemain and Ricklefs 2008, Laenen et al. 2011). Another paradigm shift stems from an increasing awareness that very long-distance dispersal was probably more frequent than previously thought. Le Roux et al. (2014) have for instance recently shown that the Hawaiian *Acacia koa* and Réunionian *A. heterophylla*—species endemic to islands at opposite ends of the planet—are possibly linked by a very unlikely recent long-distance dispersal event and may actually represent the same species. Furthermore, phylogenies that include a good representation of related continental taxa (unfortunately often still not the case, but see Carlquist et al. (2003)) provide clues for detecting the most likely continental ancestral colonizer, its geographical origin, its life form (e.g., for testing the ancestral or secondary nature of insular woodiness; Carlquist 1995, Lens et al. 2013), and its environmental affinities (e.g., for testing niche shift or niche conservatism hypotheses during diversification, Levin 2003, Wiens and Graham 2005).

Phylogenetic research also greatly improves the taxonomic treatment of island biotas that in many cases are based on outdated work by a single or few individual taxonomists, including providing species-specific haplotype networks that reveal the existence of taxonomically cryptic species. Such new information can substantially change crucial island biogeography data such as species numbers or endemism. For instance, island endemism at higher taxonomic levels has been reduced where odd endemic genera (e.g., Hawaiian *Tetraplasandra* and *Munroidendron*, Araliaceae) have been found to be nested in a widespread genus (*Polyscias*; Lowry and Plunkett 2010, Plunkett and Lowry 2010). In other cases, island endemism has increased when insular members of widespread genera have been newly recognized as distinctive endemic taxa (e.g., Hawaiian *Pleomele*, Asparagaceae, have been placed in the new endemic genus *Chrysodracon* (Lu and Morden 2014)). Such taxonomic revisions can even happen at the family level. The Hawaiian honeyeaters, long thought to be members of the South Pacific and Australian family Meliphagidae,

have been revealed as a spectacular case of convergent evolution, and they are now classified in the completely unrelated, new endemic family Mohoidae (Fleischer et al. 2008), whose closest continental relatives are the New World waxwings, silky flycatchers, and palm chats. Another striking example of the importance of accurate taxonomic information comes from the Azorean archipelago in the Atlantic Ocean. The low species richness and endemism of these islands has for some time been discussed as the ‘Azorean enigma’ (Carine and Schaefer 2010, Triantis et al. 2011). Recently the complete flora has been sequenced, allowing empirical evaluation of alternative explanations (Schaefer et al. 2011a,b).

Palaeoecology

Another methodological advance is our rapidly-improving ability to reconstruct past climates and vegetation zonation, climatic shifts, volcanic impacts, anthropogenic impacts, and even species interactions through palaeoecological research (de Nascimento et al. 2009, Wood et al. 2012, Wilmshurst et al. 2013) which is providing increasingly detailed and precise pre-human (prior to aboriginal settlers) or pre-contact (prior to European colonization) ecological baselines. Increasingly complete palaeorecords are helping to reveal the identities and ecological roles of many extinct species (Meehan et al. 2002, Steadman 2006, Cheke and Hume 2008, de Nascimento et al. 2009) and to clarify the native or non-native status of other species (van Leeuwen et al. 2008, van der Knaap et al. 2012, Craig and Porch 2013).

Overcoming Linnean and Wallacean shortfalls

Island research is expanding the scope of its geographic and taxonomic coverage (Kueffer et al. 2014), making information for biogeographic analysis increasingly comprehensive. The discovery of undescribed island species (Linnean shortfall) has significantly improved in recent decades, as has knowledge of species distributions (Wallacean shortfall). For instance, during the last 20 years, a species that is new to science has been

discovered every five days in the Canary Islands (Martín Esquivel et al. 2005), the number of described species of lemurs in Madagascar has risen from 33 to 100 (Mittermeier et al. 2008), and at least 30 endemic rodents have been discovered in the Philippines (Heaney et al. 2011, 2014). The discovery of undescribed island species, and the patterns they will reveal, though still far from complete, is progressing rapidly. For many archipelagos, regularly updated species lists (e.g., Hawaiian angiosperms² or Canarian terrestrial species³) are now freely available online and are used intensively for testing biogeographical hypotheses. And whereas land birds and flowering plants have been the taxonomic groups upon which island biogeography has traditionally relied most heavily, we are now witnessing how ferns, mosses, spiders, insects, land snails, reptiles, and mammals are receiving greater attention and providing independent insights (e.g., see Cameron et al. (2013) for land snails and Patiño et al. (2013) for bryophytes).

Theoretical and methodological advances

The increasing availability and richness of island data are resulting in major theoretical and methodological advances. The increasing access to ever-growing computational power has allowed management of huge amounts of data, and yielded new understanding of the geographical, environmental, and biotic structure for the world's ca. 20,000 islands of >1 km² (Kreft et al. 2008, Weigelt et al. 2013). Such data enable increasingly comprehensive analyses with many replicated islands, as well as multi-scale analyses that compare patterns among islands within and across archipelagos. Further information, for instance on the distribution and abundance of species at a habitat scale, will allow for progressively detailed comparative studies between island groups (Kueffer and Fernández-Palacios 2010). Another outstanding example of the disappearance of logistic and computational barriers in island biology is the

Moorea Biocode Project, a barcoding initiative to create the first comprehensive inventory of all non-microbial life in a complex tropical ecosystem (Moorea, Society Islands). One outcome of the project will be a library of genetic markers and physical identifiers for every Moorean species, available to island biologists around the world. Other interesting approaches include multi-species abundance and distribution pattern comparisons across similar ecosystems in different islands, such as the one being now carried out with EU funds for its overseas entities (Netbiome project⁴) on humid forests of Tenerife, Terceira (Azores) and La Réunion.

The new information on the biological and geological history of islands and their floras has fostered conceptual advances, with the postulation of models such as the progression rule (Funk and Wagner 1995), in which lineages diversify as they jump from older to younger islands within an archipelago, or the General Dynamic Model (Whittaker et al. 2007, 2008), which is based on the ontogenetic stages that a hot-spot island goes through. Furthermore, very valuable detailed palaeogeographical reconstructions provide a series of explicit hypotheses about past population structuring, species formation, and community assembly that can be tested with molecular and geospatial data from extant species (Gillespie and Roderick 2014). The future may produce integrative biogeographic analyses of whole species assemblies across multiple trophic levels, or of biological entities at a genotype level, and a better integration with latest theory in ecology such as neutral theory (Losos and Ricklefs 2010).

Epilogue

Islands are ideal model systems for the latest research questions and methods in all aspects of biogeography, from the evolutionary to the ecological. It is becoming feasible to do research that integrates processes at vastly contrasting temporal and spatial scales: from local coexistence and

² <http://botany.si.edu/pacificislandbiodiversity/hawaiianflora/index.htm>, last accessed 10/3/2015

³ http://www.gobiernodecanarias.org/medioambiente/piac/descargas/Biodiversidad/Listas-Especies/Lista_Especies_Silvestres.pdf, last accessed 16/3/2015

⁴ <http://island-biodiv.org>

species interactions, to regional species assembly, to large-scale and long-term biogeographical processes. The goal of the Island Biology 2014 conference in Honolulu was to launch a regular series of international island biology conferences, bringing together researchers who, by the very nature of the islands they study, face geographical barriers to communication and collaboration. Such a strengthening and expansion of the island biology community will also be of particular value to island biogeographers as they attempt to develop increasingly realistic, predictive models that explain the development of island biotas. We hope that regular meetings will help promote fruitful interactions between island biologists, who often work at the scale of the ecology and evolution of specific taxa and islands on the one hand, and biogeographers who traditionally focus on analysis of large-scale but relatively coarse general patterns on the other (Kueffer and Fernández-Palacios 2010). Finally, we should not forget that islands have suffered a hugely disproportionate amount of biodiversity loss, beginning with human colonization, and accelerating since European expansion (Whittaker and Fernández-Palacios 2007); islands today constitute the most critical arena for practical development of conservation biology and conservation biogeography (Kueffer and Kaiser-Bunbury 2014). As the world's island biologists combine their approaches, fascinating and desperately needed breakthroughs are sure to follow.

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Submitted: 11 November 2014

First decision: 05 January 2015

Accepted: 23 March 2015

Edited by Joaquín Hortal and Michael N Dawson