e-ISSN: 1948-6596 https://escholarship.org/uc/fb doi:10.21425/F59132081

OPINION

A RANT FROM THE LEVANT

Oceanic island biogeography: Nomothetic science of the anecdotal[1]

Shai Meiri

Department of Zoology, Tel Aviv University; 6997801, Tel Aviv, Israel, unchai@post.tau.ac.il, http://shaimeirilab.weebly.com/

Abstract. Islands get more than their fair share of attention from biogeographers, macroecologists and evolutionary biologists. Adding to this existing bias, I claim that oceanic islands, especially oceanic island archipelagos (and among them, especially the Hawaii, the Canaries, Azores and, of course, the Galapagos) attract much more scientific attention than the insights they offer or warrant. This focus on oceanic islands ignores other island types that may be better heuristic tools for studies of general ecological, biogeographic and evolutionary dynamics. The evolutionary and ecological dynamics of landbridge and continental islands are often as fast, dramatic, interesting and insightful, and merit more attention from island biogeographers.

Keywords: continental islands, ecology, evolution, heuristic models, island types, landbridge islands, natural laboratories, oceanic archipelagos

We love islands. Islands sound exotic and magical (Lawrence 1927, Munthe 1929), mysterious and yet benign and with a relaxing atmosphere. Pictures of blue seas, golden sands, clear skies and coconut palms come to mind (Schofield and George 1997), perhaps alongside a nice daiquiri to boot.

Island animals also kindle our imagination: we have all heard of huge tortoises, flightless birds, strange lemurs, and hobbit-like humans hunting pygmy elephants while evading dragon-sized lizards. We learn that evolutionary biology had its birth on islands with Darwin's visit to the Galapagos (Darwin 1845), and Wallace's travels in the 'Malay Archipelago' (Wallace 1868).

Zoologists (e.g. Durrell 1956), botanists, evolutionary biologists, ecologists and biogeographers are fascinated by islands, and conservation biologists, unfortunately, often need to study them (e.g. Durrell 1977, Case et al. 1998, Turvey 2009). Partly this is because they are often perceived to manifest extreme morphologies (e.g. Hedges 2008, cf. Moen and Wiens 2009, Meiri et al. 2011), ecologies (Andrews et al. 1979, Blondel 2000, Olesen and Valido 2003) and life histories (e.g. Adler and Levins 1994, Turvey et al. 2005, Covas 2012, Novosolov et al. 2013). We also like to give other reasons: islands are not just interesting in their own right but offer simple, species-poor and spatially well-delineated systems that serve as great (we say) heuristic models for the more complicated systems of the mainland (Wallace 1880 chapter XI, Mayr, 1967, MacArthur and Wilson 1967, Losos and Ricklefs 2009, Santos et al. 2016). I strongly suspect three other attributes of islands add a special allure to conducting scientific research on islands: the first is that we find them psychologically alluring. Lawrence Durrell (1953, p. 15) referred to this as 'islomania', writing that it is an "affliction of spirit… There are people who find islands somehow irresistible. The mere knowledge that they are on an island, a little world surrounded by sea, fills them with an indescribable intoxication". Simply put, we expect them to yield scientific treasures, and when conducting field work on islands we also feel isolated

1 Nomothetic: of or relating to the study or discovery of general scientific laws

from mundane day-to-day life (and can leave autoreplies saying "I am working on a remote island with very little internet access" and make it stick even in the best connected islands). The other two are well-known biological phenomena: the often extremely abundant populations found on islands (e.g. Case 1975, Schoener and Toft 1983, Novosolov et al. 2016) and the tendency of the individuals to reduce anti-predator behaviour (insular naiveté, Darwin 1845, Blumstein and Daniel 2005, Cooper et al. 2014, Brock et al. 2015). Thus often there are more of our study animals in a given area on islands, and they are easier to observe and study there. Islands are great.

Or are they? I think, that we, island biologists and biogeographers, are infatuated with islands, perhaps too much so. More importantly, I would argue (rant, if you like) that island biogeographers tend to mostly study, model, and think about oceanic islands. Ever since Lack (1947) and MacArthur and Wilson (1963), if not before (Darwin 1859), it was the oceanic island archipelagos that most stirred the imagination of generations of biogeographers. With MacArthur and Wilson (1963, 1967) also came strong infatuation with the unobtainable and unobservable: the colonization of barren islands.

There are four major ways to make an island: pour some lava upwards from the ocean floor (you can later build a coral atoll around it if you so desire), break a continent, or play with sea levels (either lower or raise them). Oceanic islands are formed by the first method, and are devoid of life at birth. So, remarkably, are the islands we rarely mention in our biogeography textbooks: those that form from lowering sea levels (eustatic changes can also create an island in a similar fashion). We don't mention or study them because they are not around any more: the last major episode when such islands were formed probably occurred at the start of the last glacial period some 120 thousands of years ago, when ice advanced and sea levels dropped, exposing areas that were just under sea level. These were probably all flooded at the end of the last ice age, and are not around to be studied today. But the other two types, land-bridge and 'continental' islands are. They are much more prevalent than oceanic islands, are present worldwide except in the heart of the oceans, and are, I would argue, much more interesting and important to study than are oceanic islands. They are not, and probably never were, empty of life: they started their ontogenies with a full suite of biota. But instead of the optimistic process of filling up with species, they probably went through the depressing one of what Diamond (1972), perhaps cynically, termed 'relaxation' through which they lost more species through extinction than they gained by colonization and cladogenesis.

We almost never follow colonization from its very onset. We have but one Krakatau – an island group that was formed recently enough to allow the study of colonization of a biologically empty island (and even this has somewhat haphazard history of studies; e.g. Thornton et al. 1988, Bush and Whittaker 1993). To study colonization we thus mainly resort to defaunation and manipulation (e.g. Simberloff and Wilson 1969, Simberloff 1976). We are very limited in our ability to empirically study the process that differentiated oceanic islands most from other island types (and thus make them interesting): colonization of 'virgin lands'. Relaxation – undoubtedly a much more prevalent process in times of anthropogenic disturbance and climate change, is rarely studied on islands (but see, e.g. Case 1975, Crowell 1986, Foufopoulos and Ives 1999, Foufopoulos et al. 2011 – mainly for land bridge islands).

Oceanic islands have distinct dynamics – they are born empty, probably get populated quickly, and have long and protracted deaths (e.g. Heaney 2000, Whittaker et al. 2008). Unless they are large enough they are likely to have little or no intra-island cladogenesis, although islands within archipelagos may have inter-island cladogenesis. Thus studies of oceanic islands (and 'island biology' conferences held) usually focus on very few systems, namely the European and USA (controlled) oceanic island archipelagos of the Canaries, the Azores, Cape Verde and Hawaii, with the emblematic Galapagos thrown in for good measure. Our general dynamic theories are thus general to the level of these five archipelagos, and

not so many other, much less well studied ones. The low number of available oceanic archipelagos (others exist – e.g. the Solomon Islands, Vanuatu, Marquesas and the Society Islands, Aleutians and Kurile Islands – but are far less well studied) means we quickly run out of further archipelagos on which to conduct external validation of biogeographic models (A.B. Phillimore, pers. comm.). I wish to neither review nor criticize either old classic or new and exciting work being carried out on oceanic islands – much of it is clever, interesting and inspiring (e.g. Savolinen et al. 2006, Patiño et al. 2015, Nogales et al. 2016, Santos et al. 2016b, Weigelt et al. 2016; a very short, random sample out of dozens of works I could cite). I argue, however, that such a small number of archipelagos makes arriving at statistically robust conclusions difficult when conflicting patterns are revealed (e.g. Nogales et al. 2016).

The large distance and unique ontogeny of oceanic islands further means that the colonizers and species evolving on these islands are unlikely to spread to other systems when the islands disappear below the sea. They are probably less likely to provide propagules for colonization of other island chains and mainland regions. Hence oceanic islands are not just ephemeral (Whittaker et al. 2008) – for most lineages they are likely to be dead ends in the longer run. Continental (e.g. Raxworthy et al. 2002, Nicholson et al. 2005) and especially land-bridge islands, are probably much more likely to provide colonizers of mainland regions, reconnect to them (Bellemain and Ricklefs 2008) and contribute to the long-term dynamics of ecological communities at scales larger than the islands themselves.

Some of the more elegant bits of science were carried out on oceanic islands. Most of the rigorous nomothetic theories developed in island biogeography seem to claim generality – but may be theories of the ephemeral and anecdotal. Are oceanic islands really the great natural laboratories (Whittaker and Fernández-Palacios 2007) they are purported to be? Within archipelagos perhaps: islands differ from others in the chain by few characteristics (age, area, habitat diversity). But they differ greatly from both other island systems and from the mainland. Far too many parameters are not shared by oceanic islands and other systems for the former to be the paradigmatic 'all else being equal' of experimental manipulations. I therefore question the paradigm (recently expressed by Triantis et al. 2016 and repeated both in their abstract and on page 2 of this work) that oceanic archipelagos "are appropriate spatiotemporal units to frame analyses in order to understand large scale patterns of biodiversity".

To the zoologist, oceanic islands are also the most impoverished of all systems: they have few land mammals, few reptiles (for me the most remote pacific islands are a barren ground of cosmopolitan parthenogenetic geckos and *Emoia* skinks; the Azores and Hawaii were terrestrial mammal and reptile free until colonized by humans) and no amphibians. Such faunistically (and probably floristically) unique environments may not be good models for other systems. They are sometimes termed 'imbalanced', but one would struggle to define 'balance' and, as Elton (1930, p.17) famously quipped, "It has the disadvantage of being untrue. The 'balance of nature' does not exist". Oceanic islands are probably just not as biologically inherently interesting as richer, more diverse systems – they are only simpler, and their simplicity does not necessarily make them good models for more complex systems.

In terms of evolution[2], oceanic island chains certainly offer some of the most emblematic examples – from the Mauritius dodo, Réunion and Rodrigues 'solitaires', through Hawaiian honeycreepers to marine iguanas, Darwin's mockingbirds and Lack's finches in the Galapagos. But are these inherently more interesting than Kodiak bears, Madagascan tenrecs, Sicilian dwarf elephants or New Zealand's eleven species of moa?

Island type certainly influences the specific evolutionary trajectories of taxa inhabiting islands (e.g. Novosolov and Meiri 2013). This influence, however, may be due to average age and isolation of different island types rather than their geologi-

2 Evolution is certainly present in MacArthur and Wilson's (1963, 1967) works, but it is sorely missed in their most cited aspect: the dynamic equilibrium model

cal and ecological histories. Furthermore, all islands probably show similar evolutionary syndromes and ecological phenomena (e.g. size, colouration and life history evolution, density changes) – with differences being quantitative rather than qualitative. Evolutionary processes and relations (e.g. coevolution in ecological networks) on oceanic islands are often much simpler because of their communities' simplicity, rather than because of their origin. Loss of dispersal abilities (see above), dwarfism (e.g. Bate 1902, Lister 1989, Meiri et al. 2008) and gigantism (e.g. Angerbjorn, 1986, Olson and James 1991, Russell and Bauer 2002, Worthy et al. 2002, Aubret and Shine 2007, Raia 2009) are common on islands of all types. Life history shifts (e.g. Tamarin 1978, Adler and Levins 1994, Blondel 2000, Raia et al. 2010, Pafilis et al. 2011, Brandley et al. 2014) and density increases (e.g. Crowell 1962, Case 1975, Rodda and Dean-Bradley 2002, Novosolov et al. 2016) similarly seem to occur on all island types. Such evolutionary phenomena probably depend more on the ecological settings of different islands (e.g. absence of predation and superabundant food in the form of marine subsidies; large or small food items e.g. lizards vs. mammals and nesting seabirds; Blondel 2000, Hasegawa 2003, Keogh et al. 2005, Russell et al. 2011, Itescu et al. 2014, Slavenko et al. 2015, Reynolds et al. 2016) than on the dynamics that brought the ecological settings about.

If anything, the higher species richness derived by the large size of large continental islands, and the temporal and spatial proximity of the mainland to land-bridge islands, may present more dynamic systems than those of most oceanic islands (not sure about those daiquiris though). Continental islands (e.g. Madagascar and New Zealand) often have just as striking incidence of endemism. Land-bridge islands harbour fewer endemics – but their young ages give us a chance of viewing extremely fast instances of evolutionary change resulting from their recent insularization (Heaney 1978, Lister 1989, Vartanyan et al. 1993, Keogh et al. 2005).

I do not question the tremendous contribution of studies of oceanic islands to the development of evolutionary biology, ecology, biogeography and conservation. Nonetheless, I think we often needlessly choose to study them over studying other island types that are often just as scientifically interesting, and perhaps more scientifically relevant models. Island biogeography as a discipline may well benefit from a shift away from the predominance of oceanic island studies to incorporate more studies of other island systems, that can offer anything from extremely simple to the staggeringly complex, while being relevant models for the study of ecology and evolution.

Acknowledgements

I thank Joaquin Hortal, his better half Guida Santos, Yuval Itescu, Dan Simberloff and Maria Novosolov for inspiring discussion. Ally Phillimore, Pasquale Raia, Panayiotis Pafilis, Richard Field, Christophe Thébaud and Kostas Triantis provided much needed criticism on earlier drafts.

References

Adler, G.H. & Levins, R. (1994) The island syndrome in rodent populations. Quarterly Review of Biology, 69, 473–490.

Andrews, R.M. (1979) Evolution of life histories: a comparison of *Anolis* lizards from matched island and mainland habitats. Breviora, 454, 1–51.

Angerbjorn, A. (1986) Gigantism in island populations of wood mice (*Apodemus*) in Europe. Oikos 47, 47–56.

Aubret, F. & Shine, R. (2007) Rapid prey-induced shift in body size in an isolated snake population (*Notechis scutatus*, Elapidae). Austral Ecology, 32, 889–899.

Bate, D.M.A. (1902) Preliminary note on the discovery of a pigmy elephant in the Pleistocene of Cyprus. Proceedings of the Royal Society of London, 71, 498–500.

Bellemain, E. & Ricklefs, R.E. (2008) Are islands the end of the colonization road? Trends in Ecology and Evolution, 23, 461–468.

Blondel, J. (2000) Evolution and ecology of birds on islands: trends and prospects. Vie et Milieu, 50, 205–220.

Blumstein, D.T. & Daniel, J.C. (2005) The loss of anti-predator behaviour following isolation on islands. Proceedings of the Royal Society of London B., 272, 1663–1668.

Brandley, M.C., Kuriyama, T. & Hasegawa, M. (2014) Snake and bird predation drive the repeated convergent evolution of correlated life history traits and phenotype in the Izu Island scincid lizard (*Plestiodon latiscutatus*). PLoS ONE, 9, e92233.

Brock, K.M., Bednekoff, P.A., Pafilis, P. & Foufopoulos, J. (2015) Evolution of antipredator behavior in an island lizard species, *Podarcis erhardii* (Reptilia: Lacertidae): The sum of all fears? Evolution 69, 216–231.

Bush, M.B. & Whittaker, R.J. (1993) Non-equilibration in island theory of Krakatau. Journal of Biogeography, 20, 453–457.

Case, T.J. (1975) Species numbers, density compensation, and colonizing ability of lizards on islands in the Gulf of California. Ecology, 56, 3–18.

Case, T.J., Bolger, A.D. & Richman, A.D. (1998) Reptilian extinctions over the last ten thousand years. In: Conservation biology for the coming decade, 2nd edition (ed. by P.L. Fielder and P.M. Kareiva), pp. 157–186, Chapman & Hall, New York.

Cooper, W.E., Pyron, R.A. & Garland, T. (2014) Island tameness: living on islands reduces flight initiation distance. Proceedings of the Royal Society of London B., 281, 20133019.

Covas, R. (2012) Evolution of reproductive life histories in island birds worldwide. Proceedings of the Royal Society of London B., 279, 1531–1537.

Crowell, K.L. (1962) Reduced interspecific competition among the birds of Bermuda. Ecology, 43, 75–88.

Crowell, K.L. (1986) A comparison of relict versus equilibrium models for insular mammals of the gulf of Maine. Biological Journal of the Linnean Society, 28, 37–64.

Darwin, C.R. (1845) The voyage of the Beagle. John Murray, London.

Darwin, C.R. (1859) On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray. London.

Diamond (1972) Biogeographic kinetics: estimation of relaxation times for avifaunas of SW Pacific islands. Proceedings of the National Academy of Sciences of the USA, 69, 3199–3203.

Durrell, G.M. (1956) My family and other animals. Rupert Hart-Davis, London.

Durrell, G.M. (1977) Golden bats and pink pigeons: a journey to the flora and fauna of a unique island. Collins, London.

Durrell, L.G. (1953) Reflections on a marine Venus. A companion to the landscape of Rhodes. Faber & Faber, London.

Foufopoulos, J. & Ives, A.R. (1999) Reptile extinctions on land-bridge islands: life-history attributes and vulnerability to extinction. The American Naturalist 153, 1–25.

Foufopoulos, J., Kilpatrick, A.M. & Ives, A.R. (2011) Climate change and elevated extinction rates of reptiles from Mediterranean islands. The American Naturalist, 177, 119–129.

Hasegawa, M. (2003) Ecological diversification of insular terrestrial reptiles: A review of the studies on the lizard and snakes of the Izu Islands. Global Environmental Research, 7, 59–67.

Heaney, L.R. (1978) Island area and body size of insular mammals: Evidence from the tri-colored squirrel (*Callosciurus prevosti*) of Southeast Asia. Evolution, 32, 29–44.

Heaney, L.R. (2000) Dynamic disequilibrium: a long-term, large-scale perspective on the equilibrium model of island biogeography. Global Ecology and Biogeography, 9, 59–74.

Hedges, S.B. (2008) At the lower size limit in snakes: two new species of threadsnakes (Squamata: Leptotyphlopidae: *Leptotyphlops*) from the Lesser Antilles. Zootaxa, 1841, 1–30.

Itescu, Y., Karraker, N. E., Pritchard, P., Raia, P. and Meiri, S. 2014. Is the island rule general? Turtles disagree. Global Ecology and Biogeography 23: 689–700.

Keogh, J.S., Scott, I.A.W. & Hayes, C. (2005) Rapid and repeated origin of insular gigantism and dwarfism in Australian tiger snakes. Evolution, 59, 226–233.

Lack, D. (1947) Darwin's finches. Cambridge University Press, Cambridge.

Lawrence, D.H. (1927) The man who loved islands. In: The woman who rode away and other stories (by D.H. Lawrence). Knopf, New York, NY, 1928.

Lister, A.M. (1989) Rapid dwarfing of red deer on Jersey in the last interglacial. Nature, 342, 539–542.

Losos, J.B. & Ricklefs, R.E. (2009) Adaptation and diversification on islands. Nature, 457, 830–836.

MacArthur, R.H. & Wilson, E.O. (1963) An equilibrium theory of insular zoogeography. Evolution, 17, 373–387.

MacArthur, R.H. & Wilson, E.O. (1967) The theory of Island Biogeography. Princeton University Press, New Jersey.

Mayr, E. (1967) The challenge of island faunas. Australian Natural History, 15, 369–374.

Meiri, S., Meijaard, E., Wich, S. Groves, C. & Helgen, K. (2008) Mammals of Borneo – small size on a large island. Journal of Biogeography, 35, 1087–1094.

Meiri, S., Raia, P. & Phillimore, A. B. (2011) Slaying dragons: limited evidence for unusual body size evolution on islands. Journal of Biogeography, 38, 89–100.

Moen, D.S. & Wiens, J.J. (2009) Phylogenetic evidence for competitively-driven divergence: body size evolution in Caribbean treefrogs (Hylidae: *Osteopilus*). Evolution, 63, 195–214.

Munthe, A. (1929) The story of San Michele. John Murray, London.

Nicholson, K.E., Glor, R.E., Kolbe, J.J., Larson, A., Hedges, S.B. & Losos, J.B. (2005) Mainland colonization by island lizards. Journal of Biogeography, 32, 929–938.

Nogales, M., Heleno, R., Rumeu, B., González-Castro, A., Traveset, A., Vargas, P. & Olesen, J.M., (2015) Seed dispersal networks on the Canaries and the Galapagos archipelagos: interaction modules as biogeographical entities. Global Ecology and Biogeography 25: 912–922.

Novosolov, M. & Meiri, S. (2013) The effect of island type on lizard reproductive traits. Journal of Biogeography, 40, 2385–2395.

Novosolov, M., Raia, P. & Meiri, S. (2013) The island syndrome in lizards. Global Ecology and Biogeography, 22, 184–191.

Novosolov, M., Rodda, G. H., Feldman, A., Kadison, A. E., Dor, R. & Meiri, S. (2016) Power in numbers. The evolutionary drivers of high population density in insular lizards. Global Ecology and Biogeography, 26, 87–95.

Olson, S.L. & James, H.F. (1991) Descriptions of thirty-two new species of birds from the Hawaiian Islands: Part 1. Non-Passeriformes. Ornithological Monographs, 45, 1–88.

Pafilis, P., Foufopoulos, J., Sagonas, K., Runemark, A., Svensson, E., & Valakos, E. D. (2011) Reproductive biology of insular reptiles: marine subsidies modulate expression of the "Island Syndrome". Copeia, 2011, 545–552.

Patiño, J., Carine, M.A., Mardulyn, P., Devos, N., Mateo, R.G., Gonzalez-Mancebo, J.M., Shaw, A.J. & Vanderpoorten, A. (2015) Approximate Bayesian com-

putation reveals the crucial role of oceanic islands for the assembly of continental biodiversity. Systematic Biology, 64, 579–589.

Raxworthy, C.J., Forstner, M.R.J. & Nussbaum, R.A. (2002) Chameleon radiation by oceanic dispersal. Nature, 415, 784–787.

Raia, P. (2009) Gigantism. In: Encyclopedia of Islands (ed. by R. G. Gillespie and D. A. Clague), pp 372–376. University of California Press, Berkeley.

Raia, P., Guarino, F.M., Turano, M., Polese, G., Rippa, D., Carotenuto, F., Monti, D. M., Cardi, M. & Fulgione, D. (2010). The blue lizard spandrel and the island syndrome. BMC Evolutionary Biology, 10, 289 doi:10.1186/1471-2148-10-289

Reynolds, R.G., Collar, D.C., Pasachnik, S.A., Niemiller, M.L., Puente-Rolon, A.R. & Revell, L.J. (2016) Ecological specialization and morphological diversification in Greater Antillean boas. Evolution, doi:10.1111/evo.12987

Rodda, G.H. & Dean-Bradley, K. (2002) Excess density compensation of island herpetofaunal assemblages. Journal of Biogeography, 29, 623–632.

Russell, A.P. & Bauer, A.M. (1986) Le gecko geant *Hoplodactylus delcourti* et ses relations avec le gigantisme et l'endemisme insulaire chez les Gekkonidae. Mesogee, 46, 25–28.

Santos, A.M.C., Field, R. & Ricklefs, R.E. (2016) New directions in island biogeography. Global Ecology and Biogeography, 25, 751–768.

Santos, A.M.C., Cianciaruso, M.V. & De Marco, P. (2016b) Global patterns of functional diversity and assemblage structure of island parasitoid faunas. Global Ecology and Biogeography, 25, 869–879.

Savolainen, V., Anstett, M.C., Lexer, C., Hutton, I., Clarkson, J.J., Norup, M.V., Powell, M.P., Springate, D., Salamin N. & Baker, W.J. (2006) Sympatric speciation in palms on an oceanic island. Nature, 441, 210–213.

Schoener, T.W. & Toft, C.A. (1983) Spider populations: Extraordinarily high densities on islands without top predators. Science, 219, 1353–1355.

Schofield, J. & George, J.J. (1997) Why study Islands? In: Island studies: fifty years of the Lundy Field Society (ed. by RA Irving, AJ Schofield and CJ Webster), pp 6–13. Lundy Field Society, Lundy Island, UK.

Simberloff, D. (1976) Trophic structure determination and equilibrium in an arthropod community. Ecology, 57, 395–398.

Simberloff, D. & Wilson, E.O. (1969) Experimental zoogeography of islands. Colonization of empty islands. Ecology, 50, 278–296.

Slavenko, A., Itescu, Y., Foufopoulos, J., Pafilis, P. & Meiri, S. (2015) Clutch size variability in an ostensibly fix-clutched lizard: effects of insularity on a Mediterranean gecko. Evolutionary Biology, 42, 129–136.

Steadman, D.W. (2006) Extinction & biogeography of tropical Pacific birds. University of Chicago Press, Chicago.

Tamarin, R.H. (1978) Dispersal, population regulation, and k-selection in field mice. The American Naturalist 112, 545–555.

Thornton, I.W.B., Zann, R.A., Rawlinson, P.A., Tidemann, C.R., Adikerana, A.S. & Widjoya, A.H.T. (1988) Colonization of the Krakatau Islands by vertebrates: equilibrium, succession and possible delayed extinction. Proceedings of the National Academy of Sciences, USA, 85, 515–518.

Triantis, K.A., Whittaker, R.J., Fernandez-Palacios, J.M. & Geist, D.J. (2016) Oceanic archipelagos: a perspective on the geodynamics and biogeography of the World's smallest biotic provinces. Frontiers of Biogeography, 8.2, e29605.

Turvey, S.T. (2009) In the shadow of the megafauna. In: Holocene extinctions (ed. by S.T. Turvey), pp 17–39. Oxford University Press, Oxford.

Turvey, S.T., Green, O.R. & Holdaway, R.N. (2005) Cortical growth marks reveal extended juvenile development in New Zealand moa. Nature, 435, 940–943.

Vartanyan, S.L., Garutt, V.E. & Sher, A.V. (1993) Holocene dwarf mammoths from Wrangel-Island in the Siberian arctic. Nature, 362, 337–340.

Wallace, A.R. (1868) The Malay Archipelago. Macmillan & Co., London.

Wallace, A.R. (1880) Island life. Macmillan & Co., London.

Weigelt, P., Steinbauer, M.J., Cabral, J.S. & Kreft, H. (2016) Late Quaternary climate change shapes island biodiversity. Nature, 532, 99–102.

Whittaker, R.J. & Fernandez-Palacios, J.M. (2007) Island biogeography. Ecology, evolution, and conservation. Second Edition. Oxford University Press, Oxford.

Whittaker, R.J., Triantis, K.A. & Ladle, R.J. (2008) A general dynamic theory of oceanic island biogeography. Journal of Biogeography, 35, 977–994.

Worthy, T.H., Holdaway, R. & Morris, R. (2002) The lost world of the moa: prehistoric life of New Zealand. Indiana University Press, Bloomington.

Submitted: 17 August 2016
First decision: 4 December 2016
Accepted: 23 March 2017
Edited by Christophe Thébaud, Richard Field and Joaquín Hortal

