

Adaptation and diversification on islands

Jonathan B. Losos¹ & Robert E. Ricklefs²

Charles Darwin's travels on HMS *Beagle* taught him that islands are an important source of evidence for evolution. Because many islands are young and have relatively few species, evolutionary adaptation and species proliferation are obvious and easy to study. In addition, the geographical isolation of many islands has allowed evolution to take its own course, free of influence from other areas, resulting in unusual faunas and floras, often unlike those found anywhere else. For these reasons, island research provides valuable insights into speciation and adaptive radiation, and into the relative importance of contingency and determinism in evolutionary diversification.

When Charles Darwin embarked on his five-year odyssey on HMS *Beagle*, a Royal Navy surveying ship, he was an inexperienced, 23-year-old gentleman naturalist. He returned as one of the rising scientific stars of his generation. Many of Darwin's experiences on this trip shaped his thinking, but none was more influential than the five weeks he spent in the Galapagos Islands.

Since Darwin's time, research on islands has continued to advance the understanding of the evolutionary process. Indeed, evolutionists have come to regard islands as laboratories of evolution because island geography lays before them the underlying mechanisms of species formation and adaptive radiation. But islands also vary in many ways, and the evolutionary proliferation of life has progressed much further on some islands than on others. The varied outcomes of evolution in island settings can indicate a great deal about how evolutionary and spatial processes have built biological diversity through the formation and differentiation of species.

In this Review, we discuss what Darwin's time in the Galapagos Islands taught him about evolution and explore what islands have shown about evolution since then. In particular, recent work on islands has demonstrated the importance of geographical isolation (allopatry) in the initial stages of species formation, the role of interactions between species in adaptive radiation, and the effects of both historical happenstance and deterministic factors in the outcome of evolution on islands. In addition, in recent years, there has been a widespread move to reconstruct phylogenetic trees for individual islands on the basis of molecular information. These phylogenies describe the history of island biotas and might provide a way to synthesize evolution and biogeography at scales that bridge single remote islands, archipelagoes and continents.

Darwin in the Galapagos Islands

Three of Darwin's observations on the plants and animals of the Galapagos Islands contributed to his realization that species are not immutable, specially created forms. First, he saw that closely related populations on nearby islands vary in appearance, as he explained in *The Voyage of the Beagle*¹: "My attention was first thoroughly aroused, by comparing together ... the mocking-thrushes, when, to my astonishment, I discovered that all those from Charles Island belonged to one species (*Mimus trifasciatus*); all from Albemarle Island to *M. parvulus*; and all from James and Chatham Islands ... belonged to *M. melanotis*."

Second, Darwin noted that the inhabitants of an island usually have close affinities with forms on the adjacent continent, rather than with

species occupying similar environments elsewhere in the world. This seemed to suggest that they were not created independently¹: "It is probable that the islands of the Cape de Verd group resemble, in all their physical conditions, far more closely the Galapagos Islands, than these latter physically resemble the coast of America, yet the aboriginal inhabitants of the two groups are totally unlike; those of the Cape de Verd Islands bearing the impress of Africa, as the inhabitants of the Galapagos Archipelago are stamped with that of America."

Third, after returning to England, Darwin was informed by the ornithologist John Gould that many of the bird species in the Galapagos Islands that seemed to belong to different families were, in fact, all related members of a single family, previously unknown to science — and now known as Darwin's finches. Darwin quickly realized the implications of such phenotypic and ecological diversity¹: "Seeing this gradation and diversity of structure in one small, intimately related group of birds, one might really fancy that from an original paucity of birds in this archipelago, one species has been taken and modified for different ends."

Almost two centuries later, knowledge of the fauna and flora of the Galapagos Islands is more complete. Darwin's observations on mocking-birds, tortoises and finches have been confirmed and greatly amplified, and many of the islands' other taxa have been shown to demonstrate the same patterns of evolutionary descent and diversification (Fig. 1). Moreover, similar examples of evolutionary diversification have been documented on islands throughout the world. Biologists now recognize that it is not the Galapagos Islands in particular, but islands in general, that present a pageant of natural experiments of great value in studying evolutionary processes.

Islands as nature's test tubes

What is so special about islands? Their small size, distinct boundaries, simplified biotas and the abundance and tameness of island inhabitants all make it easier to observe and interpret patterns of evolution. Moreover, groups of islands can function as replicates in which general evolutionary patterns can be distinguished from unique outcomes.

Two additional attributes that make islands lasting focal points for evolutionary studies — their relative youth and geographical isolation — were clearly identified by Alfred Russel Wallace², the co-originator of the theory of evolution by natural selection, in his 1881 book *Island Life*³. First, many islands are either volcanic in origin or have been completely under water at some point in their history. These islands emerge above the ocean surface as blank slates for colonization and subsequent

¹Museum of Comparative Zoology, 26 Oxford Street, Harvard University, Cambridge, Massachusetts 02138, USA. ²Department of Biology, University of Missouri - St. Louis, 8001 Natural Bridge Road, St. Louis, Missouri 63121, USA.

evolutionary diversification, on which the development of ecological and evolutionary systems can be observed from their beginnings. Each island represents a new opportunity for living forms to appear and proliferate. The first colonists, finding untapped resources and lacking the constraints of a resident biota, often diversify in novel directions. This evolutionary idiosyncrasy is enhanced by unbalanced colonization — strong dispersal abilities are not evenly distributed across the ecological spectrum of continental biotas — with the result that some ecological niches on islands are filled by diversification rather than colonization⁴.

Most mainland settings, by contrast, are packed with species, their main burst of evolutionary diversification long over. Such filled communities offer relatively few ecological opportunities, and evolutionary diversification tends to produce small variations on already successful adaptive themes. For example, the evolutionary diversification of continental cardueline finches produced species that are ecologically and morphologically similar, essentially size variations on the standard finch-like way of life of cracking seeds with a stout beak (which is not to belittle the peculiar *Loxia* crossbills). By contrast, on the Hawaiian islands, a cardueline radiation descended from an initial colonist has reproduced most of the variation in the entire order of passerine birds: warblers, grosbeaks, tanagers and creepers, as well as a number of forms (such as *Hemignathus*) that lack continental counterparts (Fig. 2).

Second, many islands and archipelagoes are distant from other land masses, and some have been isolated, with low rates of colonization, for long periods. This allows island biotas to diverge along their own evolutionary trajectories, independent of, and unconstrained by, evolutionary events unfolding elsewhere^{4,5}. For old or very isolated islands, the particular mixture of evolutionary lineages that were present when an island separated from other areas, or that arrived with the occasional colonization event, is often unique and markedly different from biotas occurring anywhere else in the world.

If the goal is to study the interplay of ecological and evolutionary processes in the generation of biological diversity, islands (and their terrestrial analogues, lakes⁶) frequently offer the best opportunities. A particularly powerful approach is to combine studies of ongoing natural selection and microevolutionary change with phylogenetic analyses of evolutionary patterns in deeper, macroevolutionary, time^{7,8}, an approach that in some cases can even be experimental⁹.

Evolutionary processes

Evolutionary diversification during adaptive radiation involves two processes: the proliferation of species from an initial ancestor to many descendants, and the adaptation of species to use different parts of the environment. Recent debate has swirled around the order in which these processes occur. Does speciation precede ecological divergence and coexistence, or does divergence drive the speciation process¹⁰? Island studies have richly enhanced the understanding of both processes and the way they are related.

Speciation

Might history have taken a different course if HMS *Beagle* had sailed a different route? Suppose, for example, that it had stopped not at the Galapagos Islands but at Cocos Island, a small, isolated island north of the Galapagos. As with the Galapagos, most endemic species on Cocos Island are related to species on nearby continental areas¹¹. But unlike the Galapagos, little species proliferation (cladogenesis) has occurred *in situ*. For example, the island has just one species of Darwin's finch, *Pinaroloxias inornata*.

It is difficult to say what Darwin would have made of the situation on Cocos Island, but much can be learned from the observation that speciation has occurred on some islands but not on others. There are almost no examples of an ancestral bird species splitting into two descendants on islands smaller than Madagascar^{12,13}, for example, and the few purported cases are debatable^{14,15}. Similarly, *Anolis* lizards have speciated profusely on the larger islands of the Greater Antilles but hardly at all on the Lesser Antilles, even though some of the islands are reasonably large (Guadeloupe has an area of 1,628 km²), have been occupied by anoles for



Figure 1 | Evolutionary diversification and adaptive radiation in the Galapagos Islands. Large ground finch, *Geospiza magnirostris* (a), sitting on an *Opuntia* cactus. Both *Geospiza* and *Opuntia* have radiated in the Galapagos Islands, as has the snail genus *Bulimulus* (shown is *Bulimulus reibischi*) (b), producing phenotypically differentiated species that have adapted to different parts of the environment. Darwin noted the inter-island variation in Galapagos tortoises (*Geochelone nigra*) (c) and mockingbirds (*Nesomimus parvulus*) (d), but similar variation occurs in many other taxa on these islands, including marine iguanas (*Amblyrhynchus cristatus*, larger lizard) and lava lizards (genus *Microlophus*, smaller lizard on head of iguana) (e). (Panels a, d and e courtesy of H. Snell (Visual Escapes); panel b courtesy of C. Parent (University of Texas, Austin).)

millions of years, and seemingly provide the range of habitats to which species have adapted in the Greater Antilles^{16–18}. Indeed, small islands formerly connected to larger land masses have substantially more species¹⁹. Speciation in Galapagos snails also occurs only on larger islands, although the area required for *in situ* speciation is smaller than for lizards or birds²⁰.

Such a lack of speciation on small islands suggests that divergent natural-selection pressures are not sufficient to split one species into two. Although there are exceptions (including the sister taxa of palms, *Howea* spp., on Lord Howe Island^{21,22}), the overwhelming absence of species splitting on small islands suggests that allopatry (geographical isolation) is required — a conclusion reached by Ernst Mayr as a result of his studies of island birds²³ — and that a minimum island size exists below which islands lack opportunities for geographical isolation. Alternatively, some proposed mechanisms of non-allopatric speciation (such as speciation across ecological gradients) in theory also require a minimum area (and population size)²⁴, but these mechanisms seem unlikely for islands as large and environmentally heterogeneous as Guadeloupe.

The importance of allopatry for speciation is also demonstrated by patterns of species generation within archipelagoes. For example, although birds do not diverge into multiple species on small islands, they do so readily on archipelagoes composed of small islands²⁵. The evolutionary radiation of Darwin's finches is the best-known example, with 13 species having been produced in the Galapagos archipelago. Detailed examination of variation among populations and microevolutionary changes occurring within populations strongly supports the classic allopatric model of speciation. Populations become isolated on different islands,

and when they become sympatric as a result of one population colonizing an island already occupied by another, either they have already attained species-level distinctiveness or ecological and evolutionary processes acting in sympatry reinforce pre-existing differences, completing the speciation process^{8,26} (Fig. 3).

Once islands exceed the speciation threshold, the rate of speciation has been shown to increase with island size, at least in Greater Antillean anoles¹⁶ and Galapagos snails^{20,27}. By contrast, island age seems to have a stronger effect than island area in some archipelagoes, with islands of intermediate age having the most species and older islands losing species by extinction as their habitats degrade from erosion and loss of area^{28–30}.

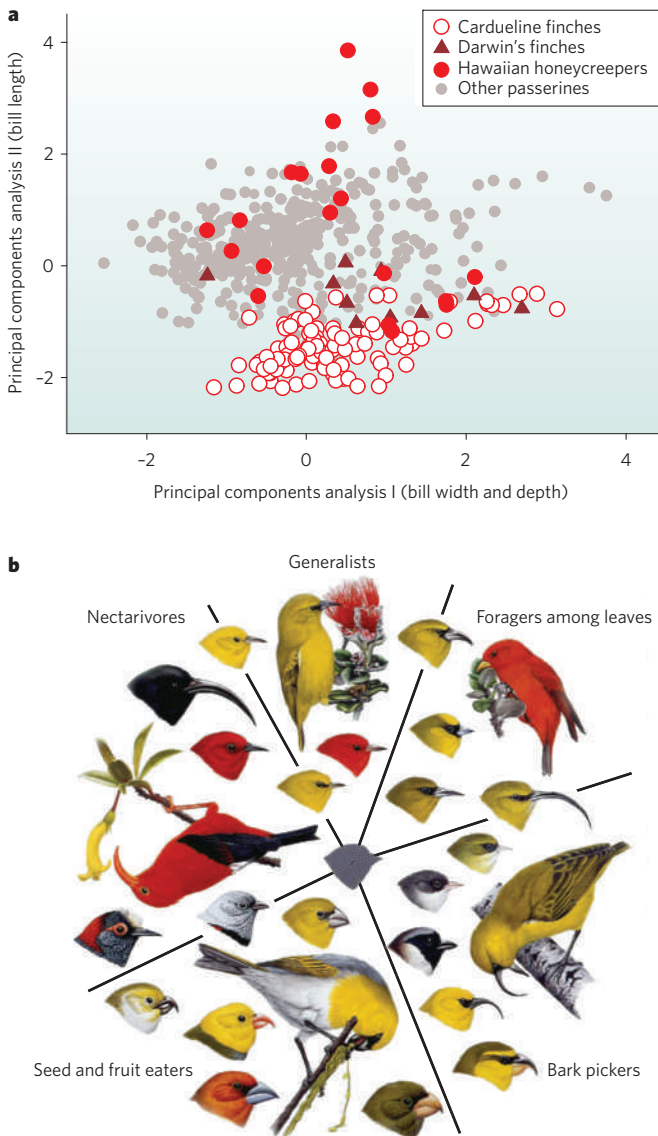


Figure 2 | Distribution of beak shapes in passerine birds, illustrating the tremendous diversification of morphology in Hawaiian honeycreepers. **a**, Graph showing variation in beak morphology in a sample of passerine birds worldwide. Variation is represented by scores on the first two axes of a principal components analysis (which derives uncorrelated axes of variation as linear combinations of the original variables). Towards the bottom right, beaks are short and stout; towards the top left, they are long and slender. Mainland cardueline finches have diversified primarily in bill width and depth, retaining the basic finch-like beak shape, whereas the Hawaiian honeycreepers have also diversified in bill length. (Data from ref. 35.) **b**, Adaptive radiation in Hawaiian honeycreepers, showing how beak shapes are adapted for particular food types. (Panel **b** reproduced, with permission, from ref. 74; courtesy of D. Pratt (North Carolina Museum of Natural Sciences, Raleigh).)

In addition, on old islands, the distributions of closely related allopatric species might expand, bringing the species into sympatry and leading to the extinction of one of the species through competition³¹.

Two explanations could account for the relationship between island size and prevalence of speciation. One possibility is that larger islands may present more opportunities for allopatric isolation thanks to their higher elevation and greater topographical and ecological complexity^{32,33}, as well as a greater opportunity for fragmentation by high sea levels or other geological events³⁴. Alternatively, island size is often correlated with ecological diversity, so larger islands might have more niche space and therefore allow the coexistence of more species, even if rates of species generation do not change with area³⁵. The evidence on Galapagos snails supports the latter possibility: vegetation diversity, which is an index of niche availability, predicts the number of within-island speciation events better than island area^{20,27}.

The extent of species diversification on islands is also affected by the degree of isolation. Gene flow between close islands prevents the divergence of populations. At the opposite extreme, populations on widely separated islands differentiate readily but rarely colonize new islands to build up local species numbers. So diversification within archipelagoes requires the appropriate correspondence of geography and dispersal ability^{36,37}.

Adaptive radiation

The evolutionary exuberance of some island clades is impressive. Every naturalist has a favourite example, perhaps the 30-odd species of silversword plant (Asteraceae) that occupy almost all terrestrial habitats in the Hawaiian islands and exhibit a vast range of morphologies, including trees, erect and compact shrubs, lianas, and branched and unbranched rosettes. Or perhaps it is the roughly 500 species of Hawaiian *Drosophila*, including species that occupy a wide variety of habitats and display a range of phenotypic variation far outstripping that of other *Drosophila*, including differences in body size, wing, leg, antennal and mouthpart morphology, and head shape^{38,39}.

Adaptive radiation is the outcome of speciation and adaptation in the context of ecological opportunity. It begins with the colonization of a species-poor environment. Allopatric speciation and subsequent recolonization of ancestral islands or areas within islands leads to the sympatry of two or more species. The abundant populations of these species now compete for resources, with selection favouring adaptations that reduce competition between species, including morphological divergence and resource specialization. Repeated again and again, this sequence of species production and character displacement in sympatry can produce a clade of endemic island taxa that are adapted and specialized to use a broad spectrum of ecological space. An unresolved question concerns the extent to which prior ecological divergence in allopatry is necessary to allow coexistence in sympatry, after which evolutionary divergence is driven by character displacement^{8,40}.

As recently as the 1980s, however, many ecologists questioned the evolutionary significance of character displacement⁴¹. Most now accept its role in diversification, and some of the best examples come from island settings^{10,42}. Islands provide unique opportunities to study character displacement because pairs of species often occur in sympatry on some islands and alone on others. The classic signature of character displacement is that species are more dissimilar in sympatry than in allopatry, although additional genetic, phylogenetic and functional data are also needed¹⁰. In a recent study on Darwin's finches⁴³, Peter and Rosemary Grant showed that natural selection in response to drought conditions favoured increased beak size (which is associated with eating larger seeds) in *Geospiza fortis* in the absence of a larger competing species, but decreased beak size (which is more suitable for gleaning smaller seeds) in the presence of such competition.

Adaptive radiation can also be brought about in other ways. For example, plant species that colonize different climatic zones might diverge physiologically and morphologically as they adapt to diverse biotic environments^{39,44–46}. Secondary sympatry of such forms could result if their differences allowed them to come back into contact and

coexist in different microclimatic niches. In addition, some adaptive radiations have produced species on multiple trophic levels — with some species eating others — suggesting that predator–prey co-evolution, as well as competitive interactions, can have a role in driving adaptive radiation¹⁰.

Clades of phenotypically disparate species are also often called adaptive radiations, but other processes, such as sexual selection (prominent in Hawaiian crickets³²) or even founder effects and genetic drift^{23,47}, can shape phenotypic divergence within a clade⁴⁸. In some cases — including radiations of birds that have diversified in beak size and shape, and radiations of lizards that have diverged in limb and toe-pad dimensions^{8,18} — the functional and ecological significance of phenotypic diversity is well understood and the adaptive basis of radiation is well established. In other cases, however, phenotypic divergence is presumed to have an underlying adaptive basis without there being supporting evidence, which ideally would come from an integration of phylogenetic, ecological and functional studies¹⁰.

Contingency and determinism

Stephen Jay Gould famously made the claim that if the tape of the history of life could be re-run, from the same starting point and in an identical environmental setting, there would be a different outcome every time⁴⁹. He argued that the contingencies of history are so great that evolutionary diversification almost always takes a unique and unpredictable course.

Independent radiations of species on different islands or island groups are not strict tests of Stephen Jay Gould's postulate because of the added level of contingency, notably variations in the ecological setting and in the initial colonists. This accidental happenstance of colonization may greatly influence the course of subsequent evolutionary diversification. Consider, for example, evolutionary diversification on the islands of New Zealand, which has occurred in the almost complete absence of mammals. As a result, the fauna of pre-human New Zealand was unlike that of anywhere else^{50,51} and included the following: a radiation of moas (flightless browsing ratites up to 3 m in height); a flightless, nocturnal, herbivorous parrot; a carrion-eating parrot; enormous raptors; giant orthopterans and weevils; copepods that lived on the forest floor; and primarily terrestrial bats that “represent the bat family's attempt to produce a mouse”⁵².

A similar story played out in Madagascar, which became isolated from the Gondwanan land mass during the Late Cretaceous period. Although Madagascar is close to Africa, many groups of birds and mammals that subsequently arose on the African continent failed to cross the gap. In their absence, many other groups took their place, including the following: radiations of herbivorous elephant birds (flightless ratites even larger than moas); lemurs ranging in size from 30 g to 200 kg, including recently extinct forms potentially convergent to tree sloths, ground sloths, gorillas and koalas; giant tortoises; chameleons, which originated in Madagascar; a radiation of carnivores related to mongooses, including one species the same size and shape as a mountain lion; hedgehog look-alikes; and radiations of birds that were originally placed in a multitude of different families⁵³. On smaller islands, the contingencies of history and opportunism of natural selection are amply demonstrated by the unusual adaptations seen in species such as the carnivorous and aquatic caterpillars of the Hawaiian islands⁵⁴ and the frugivorous, metre-long, prehensile-tailed skink (*Corucia zebrata*) of the Solomon Islands.

Nonetheless, many island radiations have produced species resembling forms that evolved independently elsewhere; that is, evolution had similar outcomes, disparate origins notwithstanding^{4,5}. A favourite pastime of evolutionary biologists is to take an island radiation, such as Darwin's finches or Malagasy vangas, and, for each of its species, identify a continental ecological analogue, each usually from a different family. However, it is important to remember that cases such as this do not count as identical outcomes of the Gouldian evolutionary replay, both because some island species have no counterparts elsewhere and because the comparisons are not with the fauna of any particular locality but with species found all over the world.

A strict definition of evolutionary determinism in adaptive radiations would include species-for-species matching⁵⁵ between independently evolving clades. Such precise evolutionary convergence is rare^{56,57} and is only accomplished among closely related clades diversifying in the same region, for which the starting conditions may be similar, satisfying the setting for Stephen Jay Gould's parable, if not its outcome. Probably the most thoroughly documented example is the radiation of *Anolis* lizards on islands in the Greater Antilles. On each island, evolutionary diversification has proceeded for the most part independently, producing on each

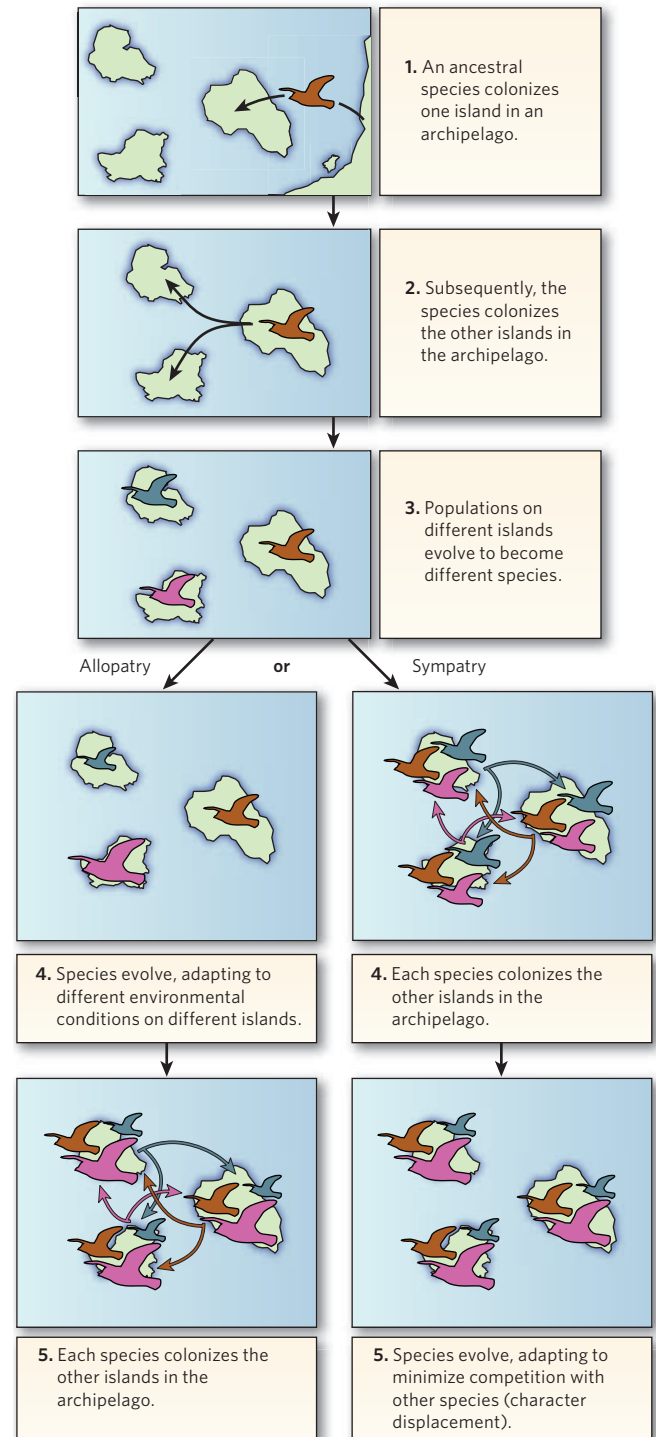


Figure 3 | Two variants of a model of allopatric speciation and subsequent sympatry in an archipelago. The top three panels apply to both models. The lower panels illustrate the possible roles of ecological divergence in allopatry (left) and character displacement in sympatry (right). (Conceptual framework from refs 8 and 16.)

island the same set of habitat specialists adapted to use different parts of the vegetation^{18,58,59} (Fig. 4). A similar phenomenon is seen among land snails of the Bonin Islands, near Japan, in which the same set of morphologically convergent habitat specialists has evolved independently on several islands⁶⁰.

Simon Conway Morris, responding to Stephen Jay Gould, argued that identical phenotypic outcomes should not be expected; instead, convergence at the level of functional niche filling should be expected, even if the way in which the niches are filled differs⁶¹. For example, in the absence of woodpeckers — birds that are specialized to extract grubs and other larvae from within woody surfaces but which disperse poorly — island species have evolved a remarkable variety of adaptations to accomplish the same end. These include the Malagasy aye-aye (*Daubentonia madagascariensis*), a lemur that uses its elongated finger to probe holes in wood; the tool-using woodpecker finch of the Galapagos (*Camarhynchus pallidus*), which probes holes with a cactus spine; the New Zealand huia (*Heteralocha acutirostris*), sadly now extinct, for which the short-billed male chiselled into wood to capture insects, and the female (which had a narrower but longer curved bill) reached into crevices inaccessible to the male to extract prey, essentially dividing between the sexes the two functions

served by the woodpecker's stout bill and long, extensible tongue; and the Hawaiian akiapolaau (*Hemignathus munroi*), which excavates holes with its short lower mandible and then extracts prey with its long and decurved upper mandible.

Deterministic patterns of evolution can also be seen in the repeated trends observed across many islands. For example, Darwin noted that most tree species make poor long-distance colonizers because of the large size of their seeds⁶². As a result, herbaceous species colonizing new islands often find themselves in open, treeless settings, where selection favours increased size to compete effectively for light. This leads to the evolution of tree-like morphologies in plant clades that never produce such phenotypes in mainland settings^{4,63}.

Another example is the 'island rule,' the tendency — contested by some⁶⁴ — for small mammals to become larger and for large mammals to become smaller⁶⁵. Island dwarfism has received the most attention, owing to the evolution on islands around the world of miniature elephants, the smallest of which was only 1 m high at the shoulder, and of hippopotamuses the size of pigs on Mediterranean islands. Interest in dwarfism was heightened by the discovery of a putative new species of small hominid that until recently lived on the island of Flores, in Indonesia⁶⁶. Less marked increases

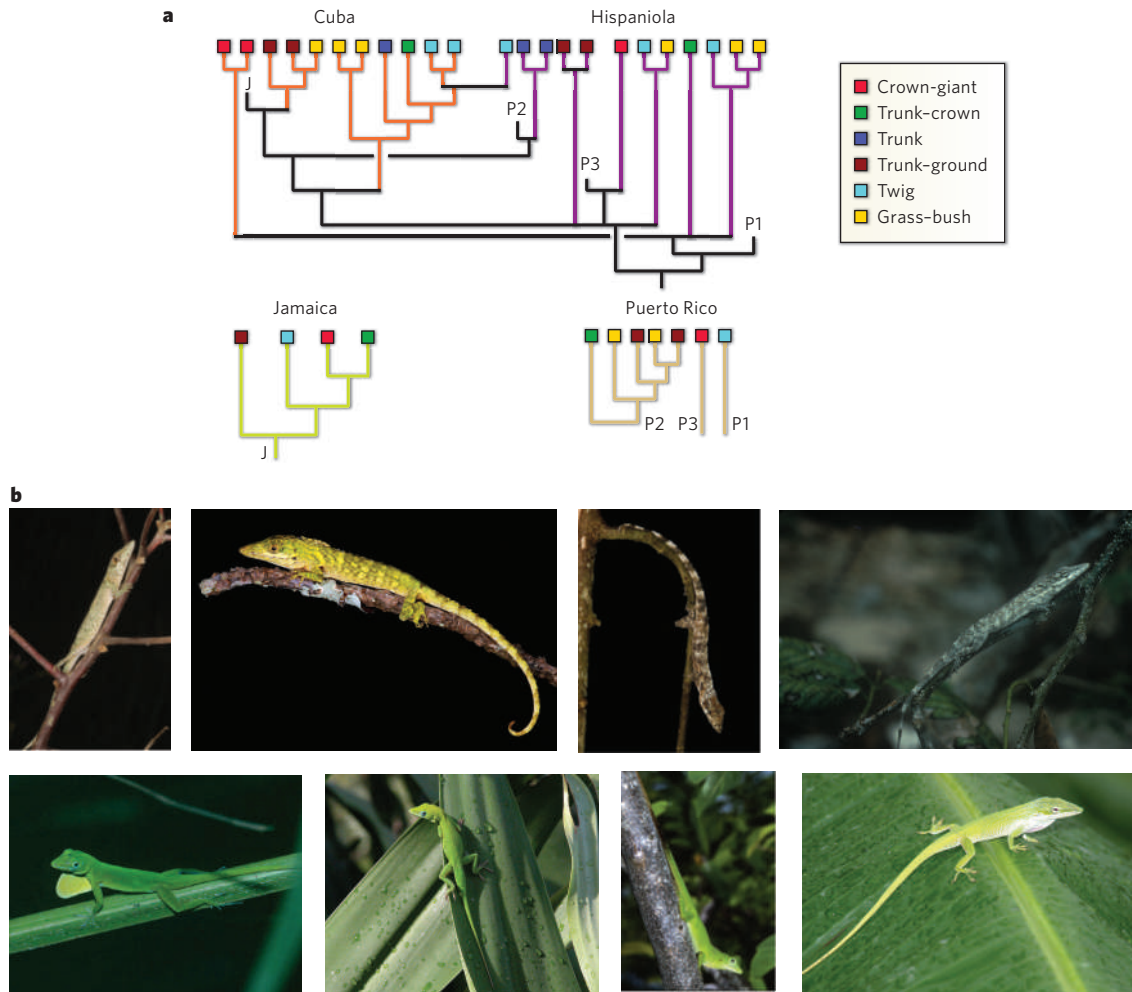


Figure 4 | Independent evolution of a set of *Anolis* lizard habitat specialists in the Greater Antilles. a, Phylogenetic tree. Horizontal black lines connect the clades on different islands and represent either overwater dispersal or ancient geological connections among islands¹⁸. Coloured lines represent the four locations. For ease of presentation, the Jamaican clade (J) and Puerto Rican clades (P1, P2 and P3) are shown separately but fit into the phylogeny at the positions marked. (Data are based on the molecular phylogeny in ref. 75.) **b**, Images show twig anoles and trunk-crown anoles. Members of each class on different islands of the Greater Antilles are not closely related to each other. Top row shows twig anoles

— from left to right: *Anolis occultus*, Puerto Rico; *Anolis insolitus*, Hispaniola; *Anolis valencienni*, Jamaica; *Anolis angusticeps*, Cuba. Bottom row shows trunk-crown anoles — from left to right: *Anolis evermanni*, Puerto Rico; *Anolis chlorocyanus*, Hispaniola; *Anolis grahami*, Jamaica; *Anolis porcatatus*, Cuba. (Images courtesy of the following individuals. Top row, left to right: A. Sanchez, M. Landestoy, L. Mahler (Harvard University, Cambridge, Massachusetts) and J. Losos. Bottom row, left to right: J. Losos, M. Losos, K. de Queiroz (National Museum of Natural History, Smithsonian Institution, Washington DC) and A. Sanchez.)

in body size, termed gigantism, are seen in many insular rodents and other small mammals. Similar evolutionary shifts occur in other groups of vertebrates⁶⁵, although some truly gigantic forms, such as moas and elephant birds, defy the rule.

Explanations for the island rule are still debated. Reduced predation on islands might release animals from being either very large, to defend themselves against predators, or very small, to hide from predators⁶⁵. Intermediate body size also might be more favourable energetically, allowing the maximum allocation of energy to growth and reproduction^{67,68}. According to this theory, selection would push mammals in the direction of the optimum, intermediate, size, but this would be countered by competitive and predatory pressures that are stronger in more species-rich mainland settings.

Other examples of deterministic patterns on islands are the evolution of flightlessness in many birds and insects, the repeated loss of dispersal abilities in both plants and animals, and the evolution of tameness in many vertebrates^{4,63} (all phenomena that were documented by Darwin^{1,62}).

Paradoxically, islands provide excellent examples of both contingency and determinism in evolution. The contingencies of lineage distribution and colonization success have seeded islands with markedly different starting points; the result is that many island faunas are unique. Yet determinism is seen at several levels, from the existence of general evolutionary trends to the evolutionary filling of the same functional roles and the occasional precise replication of communities of specialists.

Post-Darwinian islands

Many of the principles that form the modern theory of evolution, including divergence of populations in allopatry, evolutionary modification of form and function, and the diversification that occurs during adaptive radiations, were foreshadowed by Darwin thanks to his acquaintance with islands^{1,62}. Subsequent research on island biotas has contributed to the understanding of evolutionary and ecological systems in ways that were not envisaged by Darwin. Here we mention two of these: the geographical and evolutionary dynamics of island biotas, and extinction.

One of Darwin's major insights was that the flora and fauna of the Galapagos Islands were ultimately derived from elsewhere. But another century would pass before Edward O. Wilson^{69,70} inferred the dynamic interaction of dispersal and evolution from the distributions of ant taxa throughout Melanesia. Wilson realized that taxa went through cycles of dispersal to distant islands from coastal habitats, followed by adaptation to forest interior environments, loss of dispersal ability and eventual extinction. Because species might evolve secondary coastal distributions and initiate new cycles of expansion to more distant islands, Wilson called this pattern the taxon cycle. Molecular phylogenetic analyses of birds in the West Indies have provided the best evidence for taxon cycles, confirmed the temporal sequence of the distribution patterns that represent expansion and contraction phases, and strongly suggested that the cycles are generated by co-evolutionary relationships between species and their predators and pathogens⁷¹.

Darwin knew that many fossils represented extinct organisms, and he used extinction to explain the absence of intermediate forms. But direct observation was impossible, and the causes of natural extinctions (beyond major catastrophes) remain largely out of reach even now. Extinction is the converse of speciation and diversification, but its potential role as a selective agent and potentially creative force has not been resolved. Robert MacArthur and Wilson⁷² suggested that the number of species on an island achieves a steady state, with species that go extinct being replaced by colonists from elsewhere. They suggested that the rate of extinction is inversely related to island size, but neither the immediate causes of extinction nor the cause-and-effect relationship between colonization and extinction have been worked out. Islands, and particularly archipelagoes, seem to be an ideal setting for investigating extinction because of the discrete nature of island populations and, for many strongly dispersing taxa, the inference that gaps in distribution represent extinction events. The phylogenetic studies of birds in the West Indies suggested that the probability of extinction increases with

the age of an island population and, as MacArthur and Wilson supposed, is inversely related to island area⁷³.

Darwin's crucial insight was to recognize the connection between evolution and geography — that isolated lineages can evolve independently, ultimately forming new species. Although Darwin was able to infer this principle from observations of close relatives on the different islands of the Galapagos archipelago, biologists now have the tools to examine the evolutionary process more directly. Detailed population-level studies can now chart the course of evolution over short time periods, directly measuring natural selection and examining the extent to which its strength and direction change over time. In turn, phylogenetic techniques can demonstrate the histories of island biotas. These histories now allow the study of trait evolution, from which a general theory of adaptive radiation is beginning to emerge. By integrating these two approaches, biologists have the opportunity to connect pattern and process to test Darwin's postulate that natural selection is the primary engine driving evolutionary change.

One might wonder what Darwin could have accomplished with today's more complete biogeographical and palaeontological information and knowledge of evolutionary mechanisms and phylogenetic relationships. All we can say for sure is that most of what is known today about evolution and the diversification of life is the direct result of his insights. Clearly, Darwin was the right man for the time, and the fruits of his brief visit to the Galapagos Islands in 1835 remain with us. ■

1. Darwin, C. *Journal of Researches into the Natural History and Geology of the Countries Visited During the Voyage of H.M.S. Beagle Round the World, under the Command of Capt. Fitz Roy, R.N.* 2nd edn (John Murray, 1845).
2. Berry, A. & Browne, J. The other beetle-hunter. *Nature* **453**, 1188–1190 (2008).
3. Wallace, A. R. *Island Life: Or, The Phenomena and Causes of Insular Faunas and Floras, Including a Revision and Attempted Solution of the Problem of Geological Climates* (Harper, 1881).
4. Carlquist, S. *Island Biology* (Columbia Univ. Press, 1974).
5. Leigh, E. G. Jr, Hladik, A., Hladik, M.-C. & Jolly, A. The biogeography of large islands, or how does the size of the ecological theater affect the evolutionary play? *Rev. Ecol.* **62**, 105–168 (2007).
6. Fryer, G. Endemism, speciation and adaptive radiation in great lakes. *Environ. Biol. Fish.* **45**, 109–131 (1996).
7. Grant, P. R. & Grant, B. R. Unpredictable evolution in a 30-year study of Darwin's finches. *Science* **296**, 707–711 (2002).
8. Grant, P. R. & Grant, B. R. *How and Why Species Multiply: The Radiation of Darwin's Finches* (Princeton Univ. Press, 2008).
This book provides a comprehensive and up-to-date review of the evolutionary diversification of Darwin's finches.
9. Losos, J. B., Schoener, T. W., Langerhans, R. B. & Spiller, D. A. Rapid temporal reversal in predator-driven natural selection. *Science* **314**, 1111 (2006).
10. Schluter, D. *The Ecology of Adaptive Radiation* (Oxford Univ. Press, 2000).
This book gives an insightful and innovative treatment of adaptive radiation, with discussion of, and examples from, island radiations.
11. Kirkendall, L. R. & Jordal, B. H. The bark and ambrosia beetles (Curculionidae, Scolytinae) of Cocos Island, Costa Rica and the role of mating systems in island zoogeography. *Biol. J. Linn. Soc.* **89**, 729–743 (2006).
12. Diamond, J. M. Continental and insular speciation in Pacific land birds. *Syst. Zool.* **26**, 263–268 (1977).
13. Coyne, J. A. & Price, T. D. Little evidence for sympatric speciation in island birds. *Evolution* **54**, 2166–2171 (2000).
This paper demonstrates that there is lack of speciation on small islands and suggests that non-allopatric speciation does not occur in birds.
14. Ryan, P. G., Bloomer, P., Moloney, C. L., Grant, T. J. & Delport, W. Ecological speciation in south Atlantic island finches. *Science* **315**, 1420–1423 (2007).
15. Grant, P. R. & Grant, B. R. in *The Theory of Island Biogeography Revisited* (eds Losos, J. B. & Ricklefs, R. E.) (Princeton Univ. Press, in the press).
16. Losos, J. B. & Schluter, D. Analysis of an evolutionary species-area relationship. *Nature* **408**, 847–850 (2000).
17. Thorpe, R. S., Surget-Groba, Y. & Johansson, H. The relative importance of ecology and geographic isolation for speciation in anoles. *Phil. Trans. R. Soc. Lond. B* **363**, 3071–3081 (2008).
18. Losos, J. B. *Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles* (Univ. California Press, 2009).
19. Rand, A. S. Competitive exclusion among anoles (Sauria: Iguanidae) on small islands in the West Indies. *Breviora* **319**, 1–16 (1969).
20. Losos, J. B. & Parent, C. E. in *The Theory of Island Biogeography Revisited* (eds Losos, J. B. & Ricklefs, R. E.) (Princeton Univ. Press, in the press).
21. Savolainen, V. et al. Sympatric speciation in palms on an oceanic island. *Nature* **441**, 210–213 (2006).
22. Gavrillets, S. & Vose, A. Case studies and mathematical models of ecological speciation. 2. Palms on an oceanic island. *Mol. Ecol.* **16**, 2910–2921 (2007).
23. Mayr, E. *Animal Species and Evolution* (Belknap Press, 1963).
24. Gavrillets, S. & Vose, A. Dynamic patterns of adaptive radiation. *Proc. Natl Acad. Sci. USA* **102**, 18040–18045 (2005).
25. Mayr, E. & Diamond, J. *The Birds of Northern Melanesia: Speciation, Ecology, and Biogeography* (Oxford Univ. Press, 2001).

26. Lack, D. *Darwin's Finches* (Cambridge Univ. Press, 1947).
27. Parent, C. E. & Crespi, B. J. Sequential colonization and diversification of Galapagos endemic land snail genus *Bulimulus* (Gastropoda, Stylommatophora). *Evolution* **60**, 2311–2328 (2006).
The phylogenetic analysis reported in this paper indicates that the prevalence of speciation in Galapagos snails increases with island area and vegetation diversity.
28. Emerson, B. C. & Oromí, P. Diversification of the forest beetle genus *Tarphius* on the Canary Islands, and the evolutionary origins of island endemics. *Evolution* **59**, 586–598 (2005).
29. Whittaker, R. J., Triantis, K. A. & Ladle, R. J. A general dynamic theory of oceanic island biogeography. *J. Biogeogr.* **35**, 977–994 (2008).
This paper provides an important synthesis of the biological and geological factors that shape island evolution.
30. Gillespie, R. G., Claridge, E. M. & Goodacre, S. L. Biogeography of the fauna of French Polynesia: diversification within and between a series of hot spot archipelagoes. *Phil. Trans. R. Soc. Lond. B* **363**, 3335–3346 (2008).
31. Gillespie, R. Community assembly through adaptive radiation in Hawaiian spiders. *Science* **303**, 356–359 (2004).
32. Shaw, K. L. in *Hawaiian Biogeography. Evolution on a Hot Spot Archipelago* (eds Wagner, W. L. & Funk, V. A.) 39–56 (Smithsonian Institution Press, 1995).
33. Otte, D. in *Speciation and its Consequences* (eds Otte, D. & Endler, J. A.) 482–526 (Sinauer, 1989).
34. Gifford, M. E. & Larson, A. *In situ* genetic differentiation in a Hispaniolan lizard (*Ameiva chrysolaelma*): a multilocus perspective. *Mol. Phylogenet. Evol.* **49**, 277–291 (2008).
35. Lovette, I. J., Bermingham, E. & Ricklefs, R. E. Clade-specific morphological diversification and adaptive radiation in Hawaiian songbirds. *Proc. R. Soc. Lond. B* **269**, 37–42 (2002).
36. Heaney, L. R. Dynamic disequilibrium: a long-term, large-scale perspective on the equilibrium model of island biogeography. *Glob. Ecol. Biogeogr.* **9**, 59–74 (2000).
37. Parent, C. E., Caccione, A. & Petren, K. Colonization and diversification of Galapagos terrestrial fauna: a phylogenetic and biogeographical synthesis. *Phil. Trans. R. Soc. Lond. B* **363**, 3347–3361 (2008).
38. Kambysellis, M. P. & Craddock, E. M. in *Molecular Evolution and Adaptive Radiation* (eds Givnish, T. J. & Sytsma, K. J.) 475–509 (Cambridge Univ. Press, 1997).
39. Carlquist, S., Baldwin, B. G. & Carr, G. *Tarweeds and Silverswords: Evolution of the Madiinae* (Missouri Botanical Garden Press, 2003).
40. Slatkin, M. Ecological character displacement. *Ecology* **71**, 163–177 (1980).
41. Simberloff, D. & Boecklen, W. Santa Rosalia reconsidered: size ratios and competition. *Evolution* **35**, 1206–1228 (1981).
42. Dayan, T. & Simberloff, D. Ecological and community-wide character displacement: the next generation. *Ecol. Lett.* **8**, 875–894 (2005).
43. Grant, P. R. & Grant, B. R. Evolution of character displacement in Darwin's finches. *Science* **313**, 224–226 (2006).
This paper provides perhaps the best-documented example of character displacement and shows how the presence of a congeneric species changes the course of adaptation.
44. Francisco-Ortega, J., Jansen, R. K. & Santos-Guerra, A. Chloroplast DNA evidence of colonization, adaptive radiation, and hybridization of the Macaronesian fauna. *Proc. Natl Acad. Sci. USA* **93**, 4085–4090 (1996).
45. Givnish, T. J., Montgomery, R. A. & Goldsteing, G. Adaptive radiation of photosynthetic physiology in the Hawaiian lobeliads: light regimes, static light responses, and whole-plant compensation points. *Am. J. Bot.* **91**, 228–246 (2004).
46. Meimberg, H. et al. Molecular evidence for adaptive radiation of *Micromeria* Benth. (Lamiaceae) on the Canary Islands as inferred from chloroplast and nuclear DNA sequences and ISSR fingerprint data. *Mol. Phylogenet. Evol.* **41**, 566–578 (2006).
47. Carson, H. L. & Templeton, A. R. Genetic revolutions in relation to speciation phenomena: the founding of new populations. *Annu. Rev. Ecol. Syst.* **15**, 97–131 (1984).
48. Givnish, T. J. in *Molecular Evolution and Adaptive Radiation* (eds Givnish, T. J. & Systma, K. J.) 1–54 (Cambridge Univ. Press, 1997).
49. Gould, S. J. *Wonderful Life* (Norton, 1989).
50. Daugherty, C. H., Gibbs, G. W. & Hitchmough, R. A. Mega-island or micro-continent? New Zealand and its fauna. *Trends Ecol. Evol.* **8**, 437–442 (1993).
51. Goldberg, J., Trewick, S. A. & Paterson, A. M. Evolution of New Zealand's terrestrial fauna: a review of molecular evidence. *Phil. Trans. R. Soc. Lond. B* **363**, 3319–3334 (2008).
This detailed account of diversification shows that most of New Zealand's biota results from overwater colonization, rather than survival since New Zealand separated from Australia.
52. Diamond, J. in *Ecological Restoration of New Zealand Islands* (eds Towns, D. R., Daugherty, C. H. & Atkinson, I. A. E.) 3–8 (Dept Conservation, Wellington, 1990).
53. Schulenberg, T. S. in *The Natural History of Madagascar* (eds Goodman, S. M. & Benstead, J. P.) 1130–1134 (Univ. Chicago Press, 2003).
54. Rubinoff, D. Phylogeography and ecology of an endemic radiation of Hawaiian aquatic case-bearing moths (Hyposmocoma: Cosmopterigidae). *Phil. Trans. R. Soc. Lond. B* **363**, 3459–3465 (2008).
55. Schluter, D. Species-for-species matching. *Am. Nat.* **136**, 560–568 (1990).
56. Ricklefs, R. E. & Travis, J. A morphological approach to the study of avian community organization. *Auk* **97**, 321–338 (1980).
57. Wiens, J. A. Ecological similarity of shrub-desert avifaunas of Australia and North America. *Ecology* **72**, 479–495 (1991).
58. Williams, E. E. in *Lizard Ecology: Studies of a Model Organism* (eds Huey, R. B., Pianka, E. R. & Schoener, T. W.) 326–370 (Harvard Univ. Press, 1983).
59. Losos, J. B., Jackman, T. R., Larson, A., de Queiroz, K. & Rodríguez-Schettino, L. Contingency and determinism in replicated adaptive radiations of island lizards. *Science* **279**, 2115–2118 (1998).
60. Chiba, S. Ecological and morphological patterns in communities of land snails of the genus *Mandarina* from the Bonin Islands. *J. Evol. Biol.* **17**, 131–143 (2004).
61. Conway Morris, S. *Life's Solution: Inevitable Humans in a Lonely Universe* (Cambridge Univ. Press, 2003).
62. Darwin, C. *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle For Life* (John Murray, 1859).
63. Whittaker, R. J. & Fernández-Palacios, J. M. *Island Biogeography: Ecology, Evolution, and Conservation* 2nd edn (Oxford Univ. Press, 2007).
64. Meiri, S., Cooper, N. & Purvis, A. The island rule: made to be broken? *Proc. R. Soc. B* **275**, 141–148 (2008).
65. Lomolino, M. V. Body size evolution in insular vertebrates: generality of the island rule. *J. Biogeogr.* **32**, 1683–1699 (2005).
66. Brown, P. et al. A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia. *Nature* **431**, 1055–1061 (2004).
67. Brown, J. H., Marquet, P. A. & Taper, M. L. Evolution of body-size — consequences of an energetic definition of fitness. *Am. Nat.* **142**, 573–584 (1993).
68. Damuth, J. Cope's rule, the island rule and the scaling of mammalian population density. *Nature* **365**, 748–750 (1993).
69. Wilson, E. O. Adaptive shift and dispersal in a tropical ant fauna. *Evolution* **13**, 122–144 (1959).
70. Wilson, E. O. The nature of the taxon cycle in the Melanesian ant fauna. *Am. Nat.* **95**, 169–193 (1961).
71. Ricklefs, R. E. & Bermingham, E. The concept of the taxon cycle in biogeography. *Glob. Ecol. Biogeogr.* **11**, 353–361 (2002).
72. MacArthur, R. H. & Wilson, E. O. *The Theory of Island Biogeography* (Princeton Univ. Press, 1967).
73. Ricklefs, R. E. & Bermingham, E. History and the species-area relationship in Lesser Antillean birds. *Am. Nat.* **163**, 227–239 (2004).
74. Pratt, H. D. *The Hawaiian Honeycreepers: Drepanididae* (Oxford Univ. Press, 2005).
75. Nicholson, K. E. et al. Mainland colonization by island lizards. *J. Biogeogr.* **32**, 929–938 (2005).

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