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Island biogeography

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Island environments: fascinating study systems and natural laboratories

Islands have fascinated biologists since the days of Charles Darwin and Alfred Russel Wallace and before, providing the inspiration for substantial theoretical development that has advanced our understanding of global biodiversity and the mechanisms that underpin it more generally. As such, they are often termed ‘natural laboratories’, providing the ideal setting to study the interface between ecology, evolution and conservation. Part of this fascination no-doubt arises from islands harboring a disproportionate amount of global biodiversity given the amount of land-mass they occupy (roughly 15-20% of global terrestrial species present in just 3.5% of global land), including large numbers of endemic forms not found anywhere else. Interestingly, more than 25% of human languages, many of which are also threatened with extinction, are to be found on islands. In this primer, we provide an overview of the field of island biogeography, splitting it into three main sections. First, we explore some of the reasons that make islands, and the species that have evolved on them, unique and scientifically rewarding study systems for biogeographers. Second, we delve into the key island biogeography works in order to provide an introductory summary of some of the main theoretical models developed to explain species diversity patterns on islands. Unfortunately, as well as representing captivating environments to study, islands are also highly threatened systems. As such, we end with an overview of the drivers and impacts of anthropogenic environmental change on islands, providing examples of some of the extraordinary island species that humans have driven extinct.

For most people, hearing the term ‘island’ likely brings to mind remote and captivating locations of a similar type, such as Hawaii and the Galápagos. However, there are many different types of islands (Figure 1). One dichotomy is between so-called true islands –

islands of land surrounded by water (or equally areas of water surrounded by land) – and habitat islands – areas of natural habitat surrounded by contrasting (often anthropogenic) land-use types (e.g., forest fragments surrounded by agricultural land). As the global human footprint has increased, the number and range of types of habitat islands have also increased. For example, city parks have often been viewed through the lens of island biogeography; the parks representing islands of (often highly managed) ‘natural’ habitat surrounded by a sea of urban land-uses. These systems have provided an ideal setting to test island biogeographical and even evolutionary theory. For example, populations of a lizard species (*Intelligama lesueurii*) in four parks in Brisbane, Australia showed significant morphological differentiation relative to nonurban populations within a time window of less than 150 years, indicating rapid evolutionary change. There is even study of habitat islands in the marine realm, with systems such as underwater seamounts, hydrothermal vents and coral reefs all having been studied through the lens of island theory at some stage. Herein, we are focused on true islands, but even here there is a multitude of different types, including several (e.g., atolls and islands within lakes; Figure 1) that for reasons of space we do not consider here in depth. We do not yet even know the total number of true islands globally. The most recent effort resulted in an estimate 465,010 islands, with 95% being smaller than 1 km². However, considering all islands surrounded by water, including those within lakes, the total number will be well over 1 million.

An often-used classification of true (marine) islands divides them into i) oceanic islands – those that are formed over oceanic plates and have never been connected to the mainland (e.g., Hawaii, Tenerife), ii) continental-shelf islands – islands situated on the continental shelf, the majority of which have been connected to the mainland at some point in the recent (in geological time at least) past when sea-levels were lower (e.g., UK, Japan, Aegean Sea islands), and iii) (ancient) continental fragment islands – long-isolated fragments of continental rock (e.g., Madagascar). This division is a simplification, and recent island classification frameworks are based on a much larger range of island types.

The type of true island under study is important from a biological as well as a geological standpoint, as it determines how an island sources its species. Oceanic islands start with no species and gradually build up their diversity through immigration from the mainland (or other similarly remote islands) and subsequent speciation (the evolution of new species). Continental-shelf islands, many of which were once connected to the mainland by land-bridges, generally start with a full complement of species at the point of isolation, and thus lineages with historically poor dispersal ability may be present in higher proportions than on oceanic islands, where only over-water dispersal has ever been possible.

Focusing on true islands, and particularly on isolated oceanic islands, it is quickly evident why these systems are such fascinating environments to study. First, as previously mentioned, oceanic islands often support high levels of endemism (i.e., species found nowhere else). Second, these types of island are often termed ‘disharmonic’, in that their biota represents a biased subset of the mainland biota. This is the result of both dispersal and environmental filtering (Figure 2): i) only groups that possess the ability to disperse across the ocean (disregarding human translocation of species; discussed below) to oceanic islands will be present (dispersal filter), and ii) only those species that are adapted to the conditions on the islands themselves will be able to persist (environmental filter). The subsequent diversification of groups that colonise islands can also act to increase the level of

disharmony. Taken together, these filters lead to the over- and under-representation of certain plant and animal groups in oceanic island systems. For example, many mammal and amphibian groups are missing from isolated oceanic islands as a result of their reduced dispersal ability. Recent research has also found that these processes (i.e., dispersal and environmental filters) have led ecological communities (i.e., groups of similar species, such as birds, within a given area) on many oceanic islands across the world to exhibit convergence in different structural properties (e.g., greater morphological similarity than expected by chance). That is, properties of the communities of oceanic islands from different parts of the world are more similar than expected given the distance between them. Third, the prevalence in oceanic island systems of what are often grouped as ‘island syndromes’. This term refers to a wide range of phenomena, including increased flightlessness and loss of dispersal ability in birds, increased naïveté toward predators, and the shift towards woodiness in herbaceous plant groups. However, perhaps the most striking example of an island syndrome is the shift in body size of several island species relative to mainland relatives (i.e., the ‘island rule’), including the reduction in body size of larger species (e.g., a now-extinct dwarf elephant on the island of Sicily) and the increase in body size of smaller species (e.g., many insular rodent species).

Key processes in island biogeography

The biota of true islands has attracted the attention of biologists, as their natural isolation enables more straightforward evaluation of different processes related to the biota’s assembly and persistence. The key processes in (island) biogeography are generally considered to be colonisation (i.e., whereby species disperse to an island and persist for some length of time), extinction (this can be local extinction – the loss of a species from an island that survives elsewhere – or global extinction if it is an island endemic) and speciation. These processes are then linked to various island characteristics. Perhaps the two most well-studied variables in this context are island area and isolation. Area is theorised to exert influence on island diversity through multiple pathways, including larger islands supporting i) larger populations and thus reducing extinction rates, and ii) an increased diversity of habitats. More isolated islands have lower colonisation rates as they are harder for prospective colonists to reach; species with small island populations but that are also present on the mainland are also less likely to have their numbers bolstered by mainland–island dispersal (i.e., rescue effects). Isolation has traditionally been measured as the distance between an island and the nearest mainland, but recent work has stressed the importance of alternative isolation measures, such as distance to the nearest island and how islands are configured within an archipelago (i.e., a group of islands).

Island extinction and colonisation rates were brought together into a single model by ecologists Robert MacArthur and Edward Wilson in the 1960s. Their seminal monograph, ‘The Theory of Island Biogeography’ (ETIB), proposed that island richness is determined by an equilibrium between the extinction rate, which is a function of island area, and the colonisation/immigration rate, which is a function of island isolation (Figure 3). Species richness thus remains constant (i.e., at equilibrium), but species identity changes through time as species go extinct and new ones colonise. In addition, the speciation rate is predicted to vary as a positive function of both island area (larger islands have more chance for population division, and more environmental heterogeneity) and island isolation (more isolated islands have less gene flow from the mainland). A recent test of these predictions (i.e., the

relationships between extinction, colonisation and speciation rates, and island area and isolation) for birds on 41 island groups across the world using molecular phylogenetic data found them to hold.

While MacArthur & Wilson's model revolutionised the field, one limitation is that it does not take into account the dynamic nature of islands through time. In regard to volcanic oceanic islands, islands follow a roughly consistent life-cycle, first emerging from the sea, before building up to obtain maximum elevation. The island then slowly erodes and subsides, increasing in topographic complexity at first before eventually disappearing back into the sea. The key rates of colonisation, extinction and speciation, and biodiversity metrics such as species richness and percentage of endemic species, should thus also vary across this trajectory. Robert Whittaker and colleagues (including one of us) recently integrated these ideas into a new model: the general dynamic model of oceanic island biogeography (GDM). The GDM combines the core elements of the ETIB with an evolutionary time-scale that explicitly accounts for geological dynamics. The GDM predicts a hump-shaped relationship between island species richness and endemism patterns and island age, a pattern that has been found for many oceanic archipelagos that cover a wide range in island ages.

The importance of the dynamic nature of islands more generally (i.e., not just volcanic islands) has been increasingly recognised. In particular, the role that past sea-level change due to glacial–inter-glacial cycles has had on island isolation. Sea-levels were up to 120 metres lower at the last glacial maximum, leading to some islands becoming connected to the mainland (e.g., the UK), others becoming connected to each other (e.g., the merging of Fuerteventura and Lanzarote in the Canary Islands) and most of the rest becoming less isolated to some degree. The lowering of sea-levels also has a direct effect on island size: as sea-levels decrease, islands tend to become larger and have a greater elevational range. These changes had considerable impacts on island diversity and evolution.

As the above discussion indicates, island diversity is built up through a combination of ecological and evolutionary processes. Due to reduced rates of colonisation and gene flow, remote islands often support large numbers of endemic species. Island endemic species can be broadly classified into two forms: paleoendemics and neoendemics. The former are species that are endemic due to the extirpation of the mainland form following colonisation of the island. The latter are species that have evolved *in situ* on an island, and are often considered to be more prevalent on (remote) oceanic type islands, although some continental-shelf type islands are known to support high numbers of neoendemics. Some neoendemics are part of spectacular 'adaptive radiations', that is, the evolution, through adaptation to differential environmental conditions, of numerous distinct species (sometimes numbering in the hundreds) from a single ancestral species. The honeycreepers and silverswords of Hawaii are famous examples of animal and plant adaptive radiations, respectively.

Islands are often described as cul-de-sacs, places where animal and plant groups disperse to, and then undergo evolution and potentially speciation to eventually become a specialised insular group, with no re-colonisation of the mainland. This idea is exemplified by the taxon cycle model; another island biogeography model proposed by Edward Wilson. Developed during his studies of ants on various Pacific islands, Wilson's model predicts that arrivals to an island initially colonise marginal habitats and have wide distributions across these. Through time these species undergo adaptive shifts due in part to competition with newer

arrivals, becoming more specialised and adapted to the interior and central habitats of islands (eventually becoming new endemic species) and having more restricted distributions; the end point of this cycle often being extinction. Thus, the model re-enforces the idea that islands are cul-de-sacs for arriving species. The progression rule, whereby, within an archipelago, there is a pattern of colonisation from older to younger islands, each stage often accompanied by subsequent evolutionary divergence, further emphasises the cul-de-sac metaphor. However, while this is likely the case for many groups, there has been growing evidence that back-colonisation (e.g., from archipelagos to the mainland, or younger to older islands) is not as rare a phenomenon in islands as previously thought.

Island conservation

Unfortunately, while evidently fascinating, the substantial human impact on island biotas, culminating in the disproportionate number of island species extinctions, can also make islands disheartening environments to study. For instance, up to 2000 bird species are estimated to have been lost on Pacific islands following human colonisation alone, while over 90% of the endemic snail fauna of the Hawaiian Islands has gone extinct due to human actions. Indeed, more than 60% of the documented extinctions of terrestrial species since 1500 CE have been species endemic to islands. Islands are also often the sites of new species discoveries. For example, a recent expedition to little-explored Indonesian islands east of Sulawesi in 2013 and 2014 discovered ten new species and subspecies of birds (arguably the most well-known major animal group). However, newly discovered island species tend to be endangered and these ten are no exception; the Taliabu grasshopper warbler (*Locustella portenta*) for instance is estimated to survive in an area of habitat only a few square kilometres in size due to logging and wildfires.

But what drives the high anthropogenic extinction rates observed on islands? While this question could be the focus of a review in its own right, a simple answer is the combination of a multitude of threats, and characteristics of island species themselves. Focusing on the former first, Figure 4 highlights a selection of island species driven extinct (or at least severely threatened with extinction) by a range of different anthropogenic drivers.

Taking these in turn, we (i) first have *hunting*. Island species have often been hunted (e.g., for food, or for feathers and trophies) by island human communities, often to extinction. For example, the North Island giant moa (*Dinornis novaeseelandiae*) is an extinct species of bird that was endemic to New Zealand (Fig. 4a). One of the largest bird species ever to have existed, the species was hunted for food by the Polynesians who settled in New Zealand, and was driven extinct by the year AD 1500. While the issue of hunting and collecting may be more associated with human communities from the past, it is still a driver of contemporary island species declines. The striking Dracula parrot of Papua New Guinea (*Psittrichas fulgidus*) provides a pertinent example of this. The species is threatened due to the use of its feathers in various types of headdresses, garments popular with younger generations in the country, and researchers believe there are now more birds that form part of the headdresses than are left alive. ii) *Habitat loss* (e.g., deforestation to provide fuel or land for agriculture) is the largest driver of extinctions worldwide (i.e., not just on islands), but due to the isolated and small-scale nature of islands, habitat loss has had particularly severe effects on many islands. An often-provided example is the impacts of the large-scale deforestation that took place on Easter Island over a period of 500-1000 years, up to roughly AD 1600-1700. This

total deforesting of the island contributed to the extinction of a range of species, including the Toromiro tree (*Sophora toromiro*; Fig. 4b), which is currently extinct in the wild, although efforts are underway to reintroduce it to the island. iii) As humans colonised new islands, they brought with them a range of different species that often then colonised the islands, including cats, rats and goats. These *introduced species*, many of which had no natural predators or competitors on the islands, have often had devastating resultant effects on the native biota. The status of many islands as hubs in global transport networks has further exacerbated this issue. For example, *Nesophontes* was a mammal genus endemic to islands in the Caribbean. Possibly containing up to 12 species (one is pictured in Fig.4d), the genus is now believed to be extinct, with the introduction of rats to the islands by humans proposed as the most likely extinction driver. Other examples include the more than 13,000 plant species that have been introduced to Hawaii, with roughly 900 becoming established, and the observation that, of 134 extinct species of plants, amphibians, reptiles, birds and mammals listed in the 2015 IUCN Red List as having been driven extinct (at least partly) by introduced species since AD 1500, 115 were island endemics. As such, many governments and NGOs now have policies aimed at eradicating certain particularly problematic introduced species from islands. iv) One particularly destructive form of introduction relates to the human-assisted *introduction of disease vectors or diseases* themselves to islands. For example, avian malaria carried by an introduced mosquito is believed to have been a contributing factor in many of the extinctions of endemic Hawaiian honeycreepers (Passeriformes Drepanididae). Studies suggest that the Hawai'i Amakihi (*Chlorodrepanis virens*; Fig. 4c) may have evolved some degree of malaria tolerance, allowing it to repopulate forests where malaria prevalence is high.

v) *Climate change* is often described as a future driver of extinctions. However, Figure 4e shows the Bramble Cay melomys (*Melomys rubicola*), a recently extinct species of rodent endemic to a coral cay island (Bramble Cay) in the Great Barrier Reef, Australia. Declared extinct by the IUCN in 2015, it is argued to be the first mammal species to be driven to extinction by climate change. It is likely then that climate change will become a bigger driver of extinctions going forward, with small, low lying islands in areas predicted to have the highest sea-level rises being most at risk, such as many French Polynesian islands. Finally, (vi) the *interaction between human drivers and natural disturbances*. Again, due to the small-scale nature of islands, island species (particularly those on smaller islands) are often at risk from natural disturbance, such as natural variation in sea-levels and hurricanes. Human actions can increase the risk island species face from natural disturbances. For example, the Bahama Nuthatch (*Sitta pusilla insularis*; Fig. 4f), endemic to the pine forests of Grand Bahama island, in the Bahamas, was already highly threatened due to a combination of habitat loss and introduced species. Two large hurricanes that struck the island in 2016 and 2019 may have then driven it to extinction.

The negative impacts of human actions on island environments are not the only reason for the high observed extinction rates; it is also the case that island endemic species are often particularly susceptible to these actions. Island endemics by definition have small ranges (i.e., they are only found on single islands / archipelagos) and are thus more susceptible to broad-scale disturbances. In addition, many island species, particularly those on remote oceanic islands, have evolved in the absence of predators, leading to several of the phenomena listed above under the island syndromes banner, including loss of dispersal ability and increased

naïveté toward predators. As such, they were (and are) ill-prepared for the arrival of humans and many of the species humans subsequently introduced. The stories of European sailors arriving in Mauritius in the 1600s and being able to simply walk up to the dodo (*Raphus cucullatus*) and kill it for food, due to its fearlessness of humans, are a famous example. The introduction of the brown-tree snake (*Boiga irregularis*) to the island of Guam is another. This species was accidentally introduced to the island from its native range in the South Pacific shortly after World War 2, and is responsible for the extirpation of almost all the island's native bird population and many other vertebrate species (all of which evolved in the absence of any analogous predators), in addition to causing substantial economic damage through electric outages.

As well as being an ethical concern, the extinction of island species has wider implications, including impacts on ecosystem functioning and our understanding of island biology. Ecosystem function is the capacity of natural systems to provide goods and services that humans rely on. Species are integral components of this process, and thus their extinction on islands can have substantial knock-on effects in regard to how island ecosystems function. For example, a recent study of 20 archipelagos in the tropics and sub-tropics found that the non-random loss of particular types of species on islands (e.g., large-bodied and flightless species) had resulted in the significant loss of frugivorous species (i.e., species that predominantly eat fruit), including birds, reptiles (e.g., tortoises) and volant mammals (e.g., fruit bats). Large-bodied frugivorous species such as these are key dispersers of the seeds of many plant species as they are able to swallow large fruits and deposit them over large distances; thus, their loss will likely reduce the ability of many island plant species to persist long-term. Despite this study, the impact of widespread extinctions on island ecosystem functioning is poorly understood at the global scale, which is worrying given that an estimated 500 million people globally rely on island ecosystems in some manner.

As outlined above, a large amount of theory has been derived from the study of islands. However, this theory has mostly been developed without consideration of extinctions. As a result, we have little understanding at the global scale of how past extinctions have impacted what we consider to be natural (e.g., Fig. 2). For example, a recent evaluation of the evolution of flightlessness in birds found that incorporating 581 known anthropogenic bird extinctions, many of which were island endemics, increased the global number of bird species by 5%, but quadrupled the number of flightless species. Thus, our understanding of broad-scale patterns of bird evolution would be biased without accounting for extinct species. This evaluation also provides further evidence that the evolution of flightlessness has likely resulted in many island species facing increased extinction risk.

Finally, any discussion of island conservation is not complete without mentioning the role island biology has played in the development of the field of conservation science, particularly those studies focused on habitat loss and fragmentation. As the effects of anthropogenic habitat loss (particularly tropical deforestation) became apparent during the 1970s, researchers began using the ETIB to generate conservation guidelines for use in fragmented landscapes, based on the observation that deforestation often resulted in islands of forest surrounded by a 'sea' of contrasting land-use types (e.g., agriculture). This exercise had mixed success and the application of the ETIB and other island theories to the study of fragmented landscapes has largely been superseded by more nuanced frameworks, such as those that account for the fact that the land surrounding habitat fragments is not as

impermeable as the water around true islands. Nonetheless, it provides another example of the integral role islands have played in the development and evolution of varied and disparate fields in biology, a situation that is unlikely to change in the years ahead.

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Further Reading

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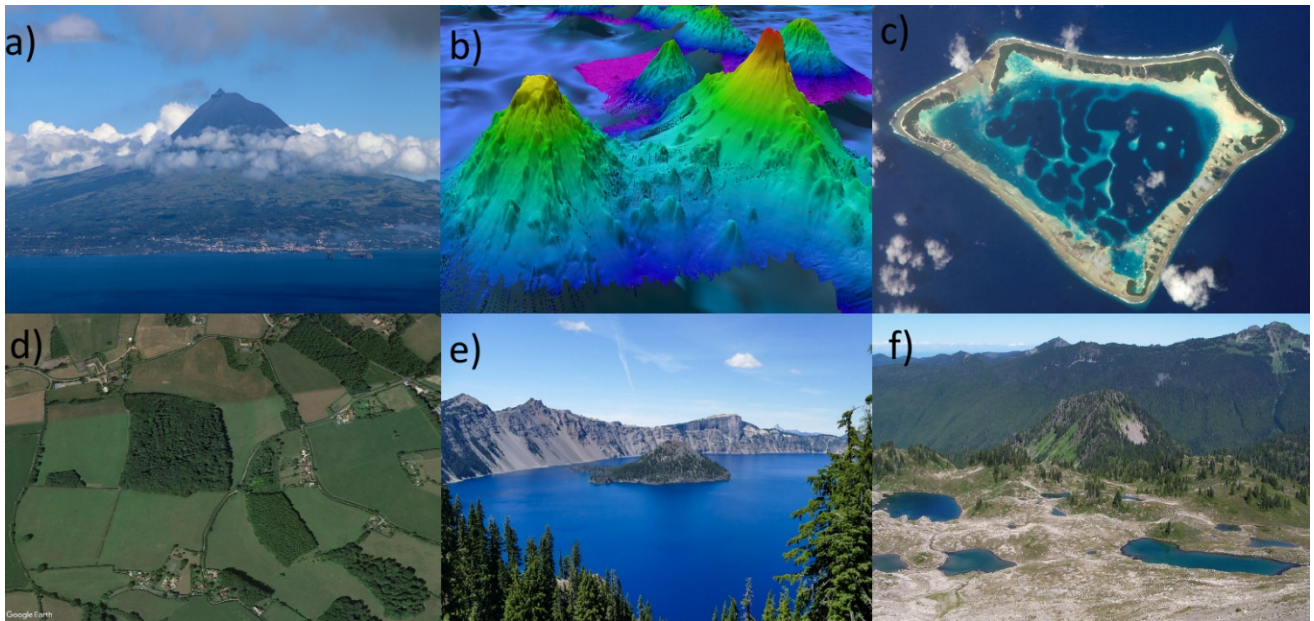


Figure 1 - Different types of island. a) Pico island, Azores, an example of a volcanic oceanic island; b) many island-type systems have been identified in the marine realm, such as seamounts (here, Pao Pao Seamount in the South Pacific); c) atolls are islands formed by coral reefs (here, South Nilandhe Atoll, Maldives); d) theory derived from true islands is often applied to forest fragment islands embedded within anthropogenic land-use types, such as agriculture (here, the UK); e) true island biogeography also includes the study of islands within lakes and not just the sea (here, Wizard island in Crater Lake, Oregon); and f) lakes can be considered as islands from the perspective of groups such as fish. Credits for images: (a) photo by Navin75, under license: <https://creativecommons.org/licenses/by-sa/2.0/>; (b) image by NOAA Ocean Exploration & Research, under license: <https://creativecommons.org/licenses/by-sa/2.0/>; (c) photo by Timo Newton-Syms, under license: <https://creativecommons.org/licenses/by-sa/2.0/>; (d) Google Earth imagery; (e) photo by Mark Smith, under license: <https://creativecommons.org/licenses/by-nd/2.0/>; (f) photo by Brian Michelsen, under license: <https://creativecommons.org/licenses/by/2.0/>.

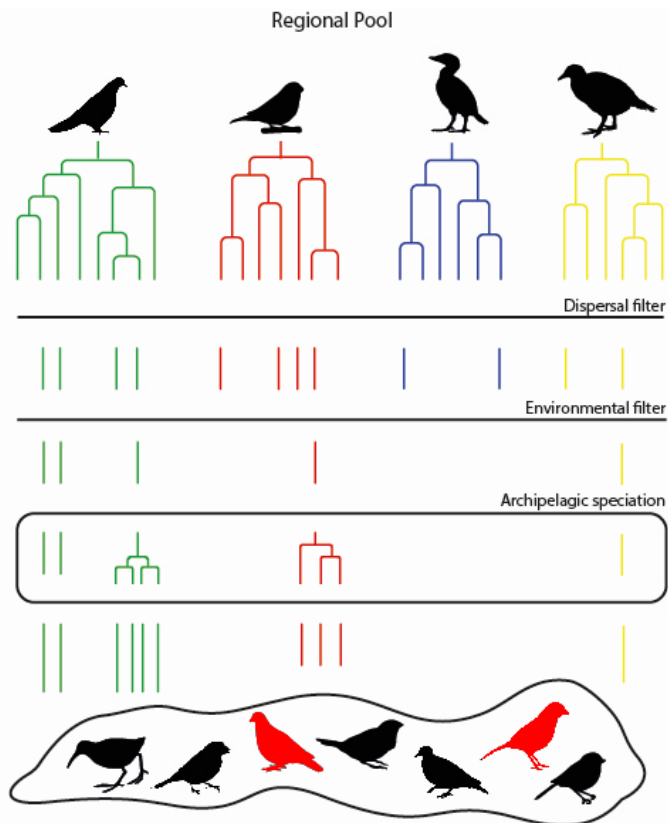


FIGURE 2. The species present on an island represent a subset of those found on the mainland (regional pool), due to having to pass through both a dispersal filter (i.e., they have to be able to get to the island) and an environmental filter (i.e., they have to be adapted to the conditions on the island in order to persist once they have arrived). Those species able to reach and persist on an island will often diverge from their mainland relatives to form new (endemic) species. Humans have driven many species on islands (e.g., those in red) extinct, influencing our interpretation of ‘natural’ island biology. Bird vector images are from phylopic.org. Top row (from left to right): the first two are available under a Public Domain Dedication 1.0 license; the third (credit to Scott Reid) under a Creative Commons Attribution 3.0 Unported license; and the fourth (credit to T. Michael Keesey (vectorization) and HuttyMcphoo (photography)) under a Creative Commons Attribution-ShareAlike 3.0 Unported license. Bottom row: all images under the Public Domain Dedication 1.0 license, except third from the right (credit to Danielle Alba) which is under the Creative Commons Attribution-ShareAlike 3.0 Unported license.

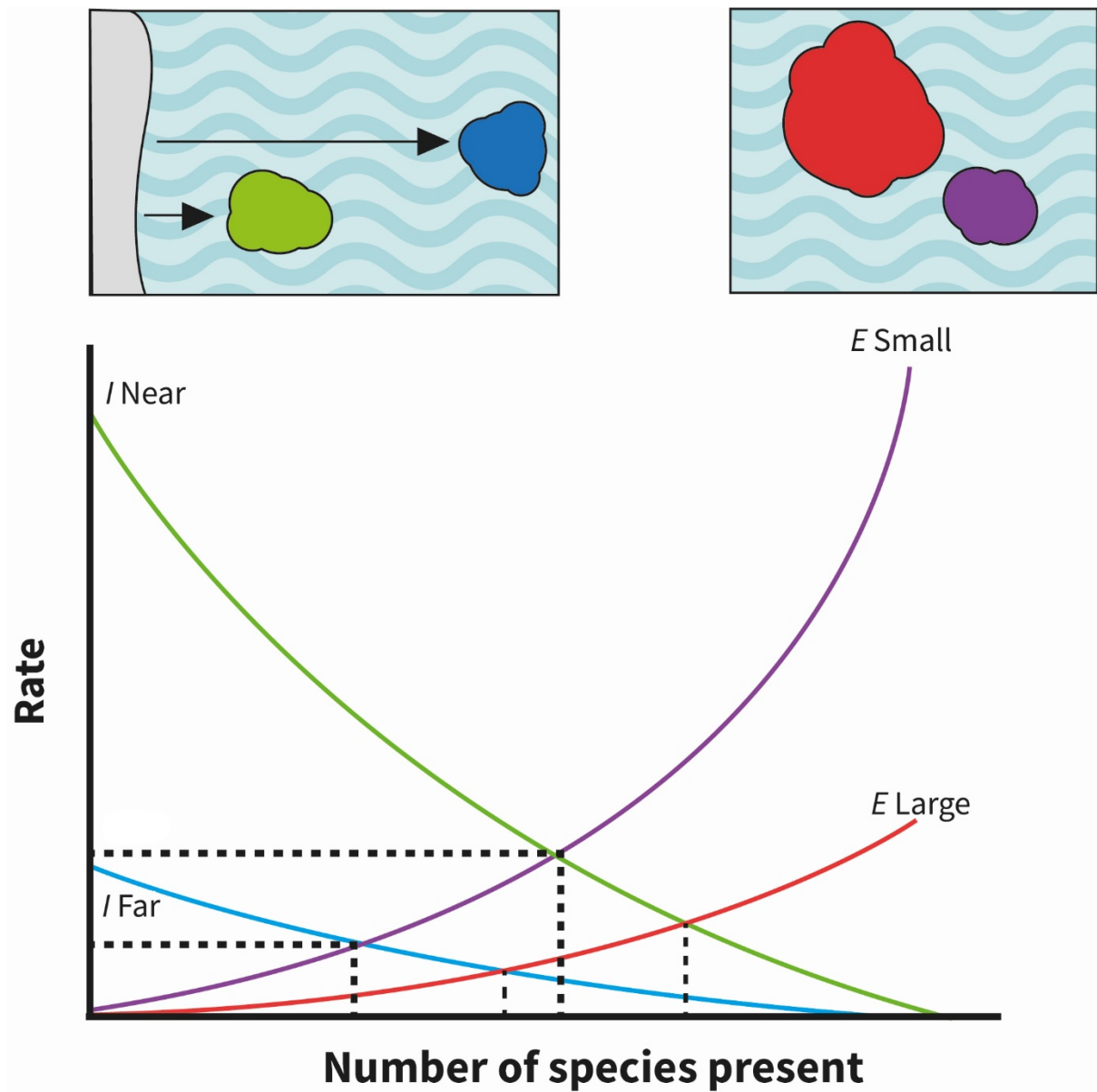


Figure 3. a) The equilibrium theory of island biogeography. Here, the equilibrium between the immigration/colonisation rate (I) and the extinction rate (E) determines the number of species present on an island. The immigration rate is a function of island isolation (with more isolated islands having lower immigration rates), and the extinction rate is a function of island area (with larger islands having lower extinction rates).

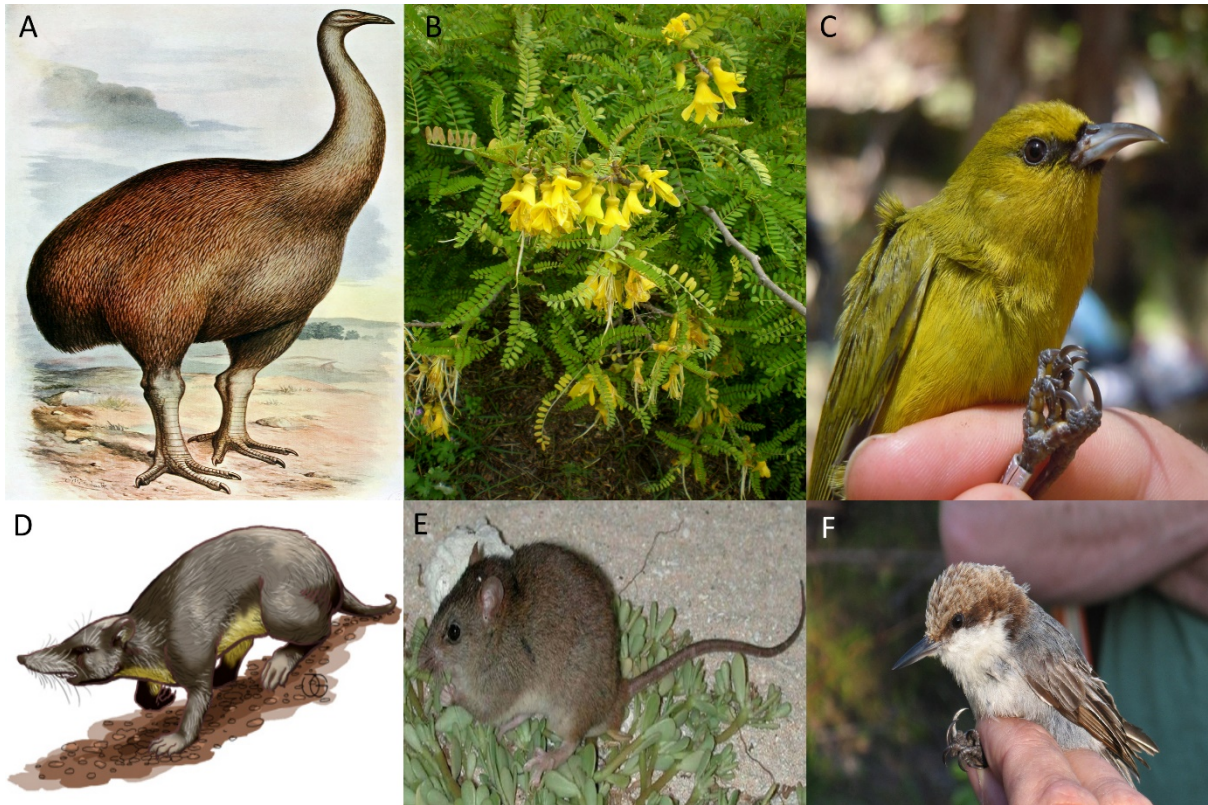


Figure 4. A selection of island species driven extinct (or at least very close to extinction), mainly as a result of different anthropogenic drivers. a) the North Island giant moa (*Dinornis novaeseelandiae*), hunted to extinction in New Zealand; b) the Toromiro tree (*Sophora toromiro*), endemic to Easter Island and currently extinct in the wild due to habitat loss; c) the Hawai'i Amakihi (*Chlorodrepanis virens*), an endemic Hawaiian bird that may have evolved resistance to the avian malaria that has been a contributing factor in the extinction of numerous Hawaiian honeycreepers; d) a *Nesophontes* species that was endemic to the Caribbean, the whole genus being driven extinct largely as a result of introduced species; e) the Bramble Cay melomys (*Melomys rubicola*), arguably the first mammal species to be driven to extinction by climate change; and f) the Bahama Nuthatch (*Sitta pusilla insularis*), endemic to Bahama Island, and perhaps driven extinct by two large hurricanes that struck the island in 2016 and 2019. Credits for images: a) image by Frederick William Frohawk and is in the public domain; b) photo by Consultaplantas, under license: <https://creativecommons.org/licenses/by-sa/4.0/deed.en>; c) photo by U.S. Fish and Wildlife Service, under license: <https://creativecommons.org/licenses/by/2.0/>; d) image by Jennifer García, under license: <https://creativecommons.org/licenses/by-sa/3.0/deed.en>; e) photo by Ian Bell, under license: <https://creativecommons.org/licenses/by/3.0/au/deed.en>; and f) photo by Thomas A. Benson, used with permission.