Island Biogeography Revisited

Matthew R Helmus and Jocelyn E Behm, Temple University, Philadelphia, PA, United States

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Abstract

For centuries, naturalists have been intrigued by islands. Patterns in island biodiversity are the basis for fundamental theories in ecology such as island biogeography theory (IBT). Under this theory, the biodiversity of islands is a function of three processes: immigration, evolution and extinction. Immigration from source pools and subsequent evolution adds biodiversity to islands. Evolution allows immigrants to adapt to island habitats and evolve into new species. In contrast, extinction subtracts species. In a natural context, these three processes are a function of island area and isolation. Larger islands have more immigration, more evolution, and less extinction and thus more biodiversity than smaller islands. Isolated islands have more evolution, but less immigration and higher extinction resulting in lower biodiversity than proximate islands. Understanding how geography influences these three processes is the focus of IBT. Here, we review the history of island biogeographic study, discuss main themes of IBT, and place IBT in the context of the Anthropocene where humans are greatly impacting island immigration, evolution and extinction.

What Is Island Biogeography?

Biogeography is the study of the processes that determine the spatial and temporal distributions of organisms and their attributes across the earth (Lomolino et al., 2017). Biogeography focuses on understanding the geological, environmental, and historic factors that determine where biodiversity is and how it is different among regions. Geographic regions are defined by physical characteristics such as mountains, climate, or water. The boundaries among regions are not always well defined and can be broad gradients that are a mix of physical characteristics between neighboring regions. However, the boundaries of islands are well delineated because they are surrounded by water making them one of the most distinct type of region.

Island biogeography is the geographic study of the terrestrial, aquatic, and marine biodiversity of islands. Island biogeography is in part determined by island type. There are two natural types of islands: "continental" and "oceanic." Continental islands reside on the continental shelf and were once connected to the continental mainland. They are often proximate to the continental mainland and as a result have many organismal groups in common with the mainland. Continental islands can be large in area such as Madagascar and Cuba. In contrast, oceanic islands are small, reside on the oceanic crust, and are mostly volcanic in origin. Atoll islands are coral reefs that have grown on top of submerged oceanic islands. Oceanic islands are often found distant from the mainland, and as a result, they are naturally isolated from the mainland and have only those species that are able to disperse long distances overwater (Helmus and Behm, 2018).

Today, island biogeography must be revisited to account for a third type of island: "artificial." Artificial islands are made by draining water from seafloors or from pilling dredged sediment and sand onto seafloors and submerged coral reefs, which can have substantial impacts to marine species (e.g., de Groot, 1979). Artificial islands can vary considerably in their isolation from the mainland, but both continental and oceanic islands tend to be larger than artificial islands. Little is known about the biodiversity of artificial islands, but most of the species are likely introduced by humans.

History of Island Biogeography

For centuries, naturalists have studied island biogeography (Lomolino et al., 2004). Carl Linnaeus (1707–78) speculated that oceans once covered the earth except for a tall mountain range that formed an island close to the equator where all species on earth were created to match different altitudinal environments on the island. As water receded, the immutable species spread to fill earth's different environments. In opposition to Linnaeus's speculation, his contemporary Georges-Louis Leclerc Comte de Buffon (1707–88) amassed volumes of information on species distributions and found that regions with similar climate and environments do not have the same plants and animals—as they would in Linnaeus's argument—instead they have distinct plants and animals indicating that species change. This concept became known as Buffon's law and was reaffirmed by other naturalists such as Joseph Banks (1743–1820) and Johann Reinhold Forester (1729–98) who circumnavigated the globe with James Cook cataloging geographically distinct species while comparing islands and the mainland. Forester was one of the first to describe positive species-area and negative species-isolation relationships; that is, the tendency of the number of species to increase as island area increases and decrease as island isolation from the mainland increases (Forster, 1778). The documentation of all these patterns led to the realization that life evolves in response to geographic and environmental factors.

Charles Darwin (1809–82) and Alfred Russel Wallace (1823–1913) independently conceived the theory of evolution by natural selection by observing island biodiversity. As evidence for evolution, Darwin argued that island species were more taxonomically similar to species on the closest continent even if the environment of that continent was different from the island. He wrote: "… there is a considerable degree of resemblance in the volcanic nature of the soil, in climate, height, and size of the islands, between the Galapagos and Cape de Verde Archipelago: but what an entire and absolute difference in their inhabitants! The inhabitants of the Cape de Verde Islands are related to those of Africa, like those of the Galapagos to America. I believe this grand fact can receive no sort of explanation on the ordinary view of independent creation" (Darwin, 1859). Alfred Russel Wallace independently devised the theory of evolution based in part on his work in Malay Archipelago. He identified a taxonomic divide located in the Malay Archipelago that delineates species derived from Southeast Asia vs. Australia due to past land connections when sea level was lower (Wallace, 1860). His book *Island Life* (Wallace, 1880) was the first comprehensive volume on island biogeography. It included a worldwide survey of island species and distinguished the two classes of islands, oceanic and continental, and how they differ in isolation. He argued that because oceanic islands are isolated from the mainland, they are colonized only infrequently by species that can immigrate over water. In contrast, continental islands are less isolated because they were once connected to the mainland and as a result have more species that are related to those of the mainland including species that did not need to colonize over water (e.g., large mammals).

Immigration, Evolution, Extinction

These early naturalists identified three fundamental processes that determine island biogeography: immigration, evolution and extinction (Lomolino et al., 2009). Species immigrate to islands by dispersing, often overwater, with some species groups more likely to disperse than other species groups (e.g., birds vs. frogs). Because the species that have immigrated to islands are often isolated from their source populations, island species evolve both by adapting to island life and randomly diverging from their source population (genetic bottleneck and drift). Finally, species naturally go extinct from islands as geography and the environment change.

Nearly a century after the early naturalists' fundamental work on island biogeography and evolution, Robert H. MacArthur and Edward O. Wilson formulated a theory of island biogeography (IBT) based on immigration, evolution, and extinction and how they are determined by island area and isolation (MacArthur and Wilson, 1963; MacArthur and Wilson, 1967; Wilson, 1969). According to the theory, the biodiversity on an island is determined by immigration to the island followed by evolutionary adaptation to the island and subsequent extinction of that biodiversity. For simplicity, the measure of biodiversity often used is species richness (i.e., number of species). Immigration increases island species richness, and evolution, if it leads to vicariant speciation (i.e., the splitting of one species into two species), also increases species richness. Extinction of species from the island reduces species richness. Under IBT, the rates of these processes are determined by island area and isolation (**Fig. 1**). While other geographic and environmental factors such as island elevation, latitude, age, and habitat heterogeneity certainly influence

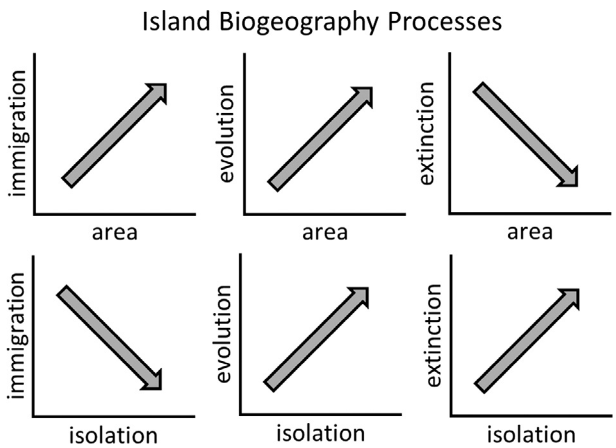

Fig. 1 Island biodiversity is determined by three fundamental biogeographic processes: immigration, evolution, and extinction. These three processes vary with island area and isolation from source pools of immigrants. *Arrows* depict relationship direction.

island biodiversity; area and isolation are still considered the most important explanatory factors (Whitehead and Jones, 1969; Heaney, 2007; Whittaker et al., 2008; Warren et al., 2015).

Island Area and Isolation

Island area is typically defined as the amount of two-dimensional terrestrial surface area, and it affects all three biogeographic processes. Larger islands have more immigration because larger islands are a larger target for dispersing individuals to land. Larger islands have more resources, habitats and space for populations to evolve and speciate. Similarly, extinction is lower on larger islands because there are more resources and space for populations to grow large and be less prone to stochastic extinction events (**Fig. 1**).

Island isolation is defined by an island's distance from potential sources of colonists. Common metrics of isolation range from simple metrics of just the distance to the nearest continent, or more complex metrics that include distances to larger islands, island groups, or prevailing currents (Weigelt and Kreft, 2013). Like area, island isolation affects all three biogeographic rates (**Fig. 1**). The primary influence of isolation is on immigration rates whereby isolated islands tend to have lower immigration than proximate islands. Evolution is also higher on more isolated islands because colonists are isolated from gene flow from the source population and thus evolve independently (Heaney, 2000; Pinheiro et al., 2017). Extinction is also higher on isolated islands because populations on isolated islands cannot be rescued from extinction by immigration from source populations (Brown and Kordric-Brown, 1977).

According to IBT, the maximum number of species that an island can contain is called its saturation point. This point is determined by island area and the number of species in the species pool; that is, the total number of species that could potentially colonize the islands. Due to speciation and extinction occurring in source areas, island species pools are not static. In the extreme case, all species from the pool can immigrate to and establish on an island, but this is never the case in nature. The saturation points of islands are determined by island area with larger islands having higher saturation points than smaller islands because larger islands have higher immigration, higher evolution that leads to vicariant speciation, and lower extinction.

Island isolation determines how close an island of a given size is to its saturation because isolated islands have lower immigration and higher extinction. When the effects of area and isolation on the three rates are in balance, then the island is said to have reached its equilibrium point. In the Anthropocene, humans are modifying immigration, evolution and extinction and shifting island equilibrium points.

Immigration Is Higher Due to Human Introductions

The rate at which nonnative, exotic (i.e., alien) species are being introduced to islands is increasing. The richness of birds, mammals, lizards, plants and invertebrates have all greatly increased on islands (Sax et al., 2002; Dawson et al., 2017). Exotic species have been introduced both intentionally and unintentionally by humans to islands for centuries, but today due to global trade, exotic immigration rate is currently the highest ever seen, and the species that are immigrating are coming from long distances.

By introducing exotic species at higher rates, humans are essentially decreasing island isolation (Helmus et al., 2014; Moser et al., 2018). For example, while the richness of native anole lizards in the Caribbean is lower on isolated islands, the richness of exotic anoles is higher on isolated islands. This is expected according to IBT because isolated islands should be farther from their saturation point and can thus gain more species than less-isolated islands closer to their saturation points when immigration rate increases. Human introduction of anole species has essentially increased anole immigration rate. Today, instead of geographic isolation limiting exotic immigration, it is economic isolation. Economic isolation is measured as the degree that islands are connected to human trade such as shipping traffic. In the Caribbean, islands that are the least connected by shipping trade have the lowest immigration rates of exotic anole species (Helmus et al., 2014).

By introducing exotic species from long distances, humans have expanded the potential species pool of immigrants (Seebens et al., 2018). In the past, species mostly immigrated to islands from the nearest mainland or from nearby islands. For example, the Caribbean has many native gecko lizard species found across all the islands. Like most Caribbean reptiles, most native gecko species of the Caribbean are derived from South America (Hedges, 2006). Today, the Caribbean has been colonized by several exotic gecko species, many from tropical Asia, Africa and the Mediterranean. The long-distance immigration of the exotic geckos began during European colonialism that moved many people and products among hemispheres essentially expanding the species pool of geckos for Caribbean islands (Perella and Behm *in review*).

Evolution in Response to Human Impacts

Human impacts are a strong selective force acting on native island biodiversity. Humans alter species interactions by introducing species and altering habitats by removing native vegetation, building structures and transforming landscapes. If native species can evolve in response to these impacts, then they are less prone to extinction. However, island species are considered to have less adaptive genetic variation than mainland species thus reducing their potential for evolution (Frankham, 1997). Regardless, native species on islands have been shown to adapt to human impacts.

Introduced species are a major force that drives evolution on islands (Mooney and Cleland, 2001; Strauss et al., 2006). For example, the mosquito *Culex quinquefasciatus* is a vector for avian malaria (*Plasmodium relictum*). Both were introduced to the Hawaiian Islands in the 1800s (Atkinson and LaPointe, 2009). The introduction of this disease greatly decreased native bird populations particularly Hawaiian honeycreepers, but this decrease acted as a selective force driving resistance to the disease in amakihi honeycreepers (Foster et al., 2007). Other examples of evolution of native island species in response to introduced species include native island plants that have evolved resistance to introduced herbivores (Vourc'h et al., 2001) and lizards that evolved different behavior and morphology in response to the introduction of lizard competitors and predators (Losos et al., 2006; Stuart et al., 2014). Introduced species also evolve following introductions to islands. For example, introduced plants have evolved reduced dispersal ability on islands similar to the reduced dispersal ability seen in native island plants (Cody and Overton, 1996) and introduced plants often adapt to novel island habitats (e.g., Dlugosch and Parker, 2008). Similarly, introduced lizards adapt their morphology in response to the novel habitats provided by islands (Herrel et al., 2008).

While introduced species can adapt to island habitats, resident island species also adapt to human alterations to their habitat. Urbanization is a strong selective force on islands (Johnson and Munshi-South, 2017). For example, *Anolis cristatellus* lizards on Puerto Rico naturally perch and climb on trees, but in developed areas of the island, lizard phenotypes have shifted to be better adapted to perch on human structures such as tiled walls (Winchell et al., 2018). *Aedes albopictus* mosquito populations in urban areas on Réunion Island are genetically differentiated from forested areas; urban areas provide human hosts and larval development sites that are different from unpopulated and undeveloped forested areas (Delatte et al., 2013).

We hypothesize that evolution of native island species in response to human impacts should be higher on larger islands and lower on isolated islands. The rationale for this hypothesis is on how area and isolation naturally affect island biodiversity. Larger islands have species with larger population sizes, thus species on large islands on average should have more phenotypic and genetic variation on which evolution can act and have more refuge from human impacts that provide time for adaptations. In contrast, smaller islands have smaller populations with less variability and less refugia from human impacts especially if those impacts are island wide. Isolated islands have low native biodiversity derived from few immigration events that can cause genetic bottlenecks that reduce adaptive genetic variation. Further, the biodiversity on isolated islands has often evolved in the absence of intense predation, herbivory and disease. Antipredator and other defenses are energetically costly and are lost from island populations released from such antagonistic interactions; a process termed the evolution of island-tameness. As a result, the ability to withstand and adapt to human impacts such as introduced predators before going extinct should be lowest on isolated islands. While the influence of island area and isolation on evolution in the Anthropocene has not been well studied, one example exists. Populations of Aegean wall lizards (*Podarcis erhardii*) across the Greek Cyclades are more tame on small and isolated islands that do not have introduced predators, while those with predators are less tame (Brock et al., 2015).

Human-Caused Extinction Is Higher on Islands

Islands make up only about 5% of the total land area on earth, yet over 60% of all known human-caused extinctions come from islands (Tershy et al., 2015). Island species are more threatened with extinction than mainland species, and much of this extinction is due to invasive predators such as cats and rats (Blackburn et al., 2004; Medina et al., 2011; Spatz et al., 2017). Island extinctions have been occurring throughout human history. For example, one of the best-known extinctions is the dodo bird once found only on the island of Mauritius. This bird was large and unafraid of humans and did not have natural defenses to predators. As a result, when Europeans colonized the island, they drove it to extinction through hunting and by introducing mammals such as cats and rats that fed on dodo eggs and chicks (Fuller, 2004). Bird extinctions on islands have been high. Polynesian colonization of the Hawaiian Islands precipitated the extinctions of several bird species due to introduced mammals, hunting, and deforestation, but then European colonization brought a second round of bird extinctions (Boyer, 2008). Similarly, extinction on Madagascar had been in two phases. First, prehistoric human colonization coincided with the extinction of giant lemurs and other megafauna, and today, resource extraction and illegal deforestation and hunting are causing Madagascar to have one of the highest extinction rates on earth (Burney, 2004; Perez et al., 2005; Jones et al., 2019).

The effect of island isolation on extinction is clear. Isolated islands have higher Anthropocene extinction rates than less isolated islands. This is thought to be due to genetic bottlenecks, island tameness, and increased island endemicity that increases extinction susceptibility on isolated islands. In contrast, the effect of area on extinction rate is less clear. Smaller islands naturally are theorized to have higher extinction rates, and many small islands have seen high extinction rates. However, because larger islands have more endemic species and more people, larger islands also can have very high extinction rates. This unclear effect of area on extinction may be due to when extinction rate is determined, in the past or in the present. For example, birds that have already gone extinct disproportionately come from small islands, but birds that are threatened with extinction currently are more likely to be found on larger islands (Blackburn et al., 2004).

Island Biogeography Revisited for the Anthropocene

Like past biogeographers who built upon the research of early naturalists, today's researchers of island biogeography build upon vast amounts of published data. Many of the studies on island biogeography in the Anthropocene aggregate large data sets (e.g., Blackburn et al., 2004; Helmus et al., 2014; Moser et al., 2018; Silva-Rocha et al., 2019). These studies have identified three major trends that make it necessary to revisit island biogeography. First, island equilibrium points are increasing in the Anthropocene. While extinctions on islands are high, the number of introduced species on average is much greater than the number of extinct native species. Second, island evolutionary history is being obscured in the Anthropocene. Area and isolation created measurable evolutionary signatures on island biota, but native species are adapting to human impacts and introduced species are from new evolutionarily distinct species pools. Finally, economic geography has become more important than physical geography in determining island biogeography. The economic isolation of islands now determines immigration rates more than geographic isolation, while the level of development and habitat loss for agriculture and resource extraction that an island undergoes determines extinction rates. We do not know exactly what island biodiversity will look like in the Anthropocene, but what is clear is that it will differ from the natural biogeography of the past.

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