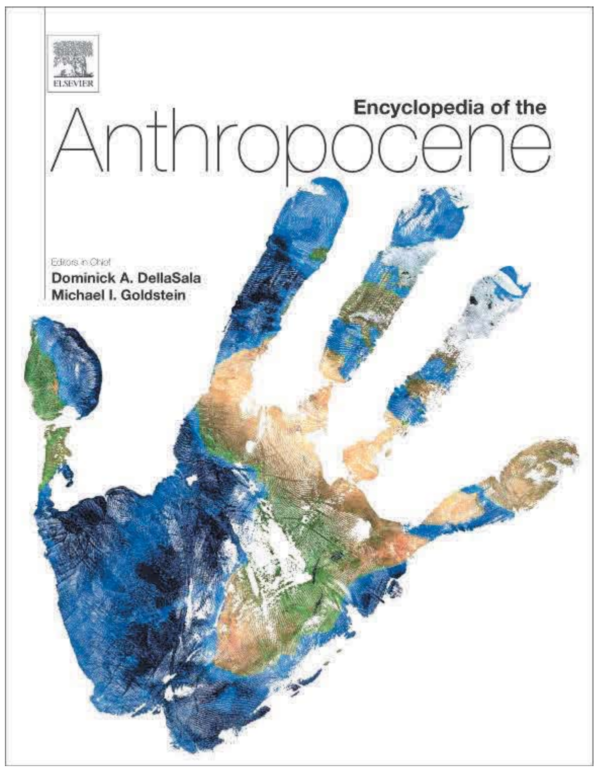

Helmus M.R., and Behm J.E. (2018) Anthropocene: Island Biogeography. In: Dominick A. DellaSala, and Michael I. Goldstein (eds.) The Encyclopedia of the Anthropocene, vol. 3, p. 37-43. Oxford: Elsevier.

Anthropocene: Island Biogeography

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What Is an Island?

Islands are land areas surrounded by water and are differentiated from the seven continents by their smaller size. For example, Greenland, the largest island, is 3.6 times smaller than Australia, the smallest continent. There are three major types of islands that are surrounded by seawater and are formed in unique ways each with their own unique properties: continental, oceanic, and artificial.

Continental islands reside on the continental shelf and were once connected to the mainland but became separated through one of two processes. In the first process, tectonic plate movement and rifting causes continental islands to split off from continents (e.g., Puerto Rico, **Fig. 1A**). In the second process, continental islands are isolated from continents by the inundation of low-lying areas by seawater (e.g., Great Britain). Common naturally occurring subtypes of continental islands are: tidal islands that are intermittent continental islands where land connecting the island to the mainland is underwater at high tide; and barrier islands made of sediment, sand, rock and coral that has accumulated on the continental shelf, parallel and close to the mainland due to ocean currents, inundated sand dunes, or glacier deposition. For example, Long Island, New York, is a barrier island formed from the deposition of sediment and rock from a melting glacier.

Oceanic islands reside on the oceanic crust and are mostly volcanic in origin although a few oceanic islands also formed from the uplift of the oceanic floor. A common subtype of oceanic islands are coral atolls formed by coral reefs growing on submerged lava and/or uplifted crust (**Fig. 1B**).

Artificial islands are novel to the Anthropocene and are made by draining water from seafloors and/or from piling material onto seafloors or submerged coral reefs (e.g., Fiery Cross Reef Island built by China in the South China Sea: **Fig. 1B**, the Palm Islands of Dubai: **Fig. 1C**).

In general, continental islands are larger and closer to the mainland than oceanic islands, with barrier and tidal islands being very close to the mainland indeed. Both continental and oceanic islands tend to be larger than artificial islands, yet artificial islands can vary considerably in their distance from the mainland with respect to the other two island types.

What Is Island Biogeography?

Biogeography is the study of the processes that determine the spatial and temporal distributions of organisms and their attributes, like genetics and traits, across the earth. Island biogeographers study biogeography across islands. Although naturalists had documented endemic species on islands for centuries, comparative analyses of island species began in earnest when Charles Darwin used island species to surmise the theory of evolution via natural selection. He deduced that endemic island species are most similar to species on the closest continent rather than the species on more distant islands with similar environments.

> The most striking and important fact for us in regard to the inhabitants of islands, is their affinity to those of the nearest mainland, without being actually the same species . . . 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 Archipelagos: 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; whereas on the view here maintained, it is obvious that the Galapagos Islands would be likely to receive colonists, whether by occasional means of transport or by formerly continuous land, from America; and the Cape de Verde Islands from Africa; and that such colonists would be liable to modification;—the principle of inheritance still betraying their original birthplace (quoted from On the Origin of Species by Charles Darwin 1859).

This idea that island biodiversity is a function of the influence of geographic location on colonization from the mainland was incorporated into island biogeography theory (IBT), a dominant theory used in island biogeography research to explain patterns of species richness (i.e., the number of species) across islands (MacArthur and Wilson, 1967).

Species Richness = Colonization + Speciation – Extinction

According to IBT, the species richness on an island is determined by three biogeographic processes: colonization, speciation, and extinction (**Fig. 2**). Colonization and speciation add species and increase species richness, whereas extinction subtracts species and reduces species richness. For example, if two islands have equal speciation and extinction rates, the island with a higher colonization rate will have the highest species richness.

 https://doi.org/10.1016/B978-0-12-809665-9.09856-6

Encyclopedia of the Anthropocene, (2018)

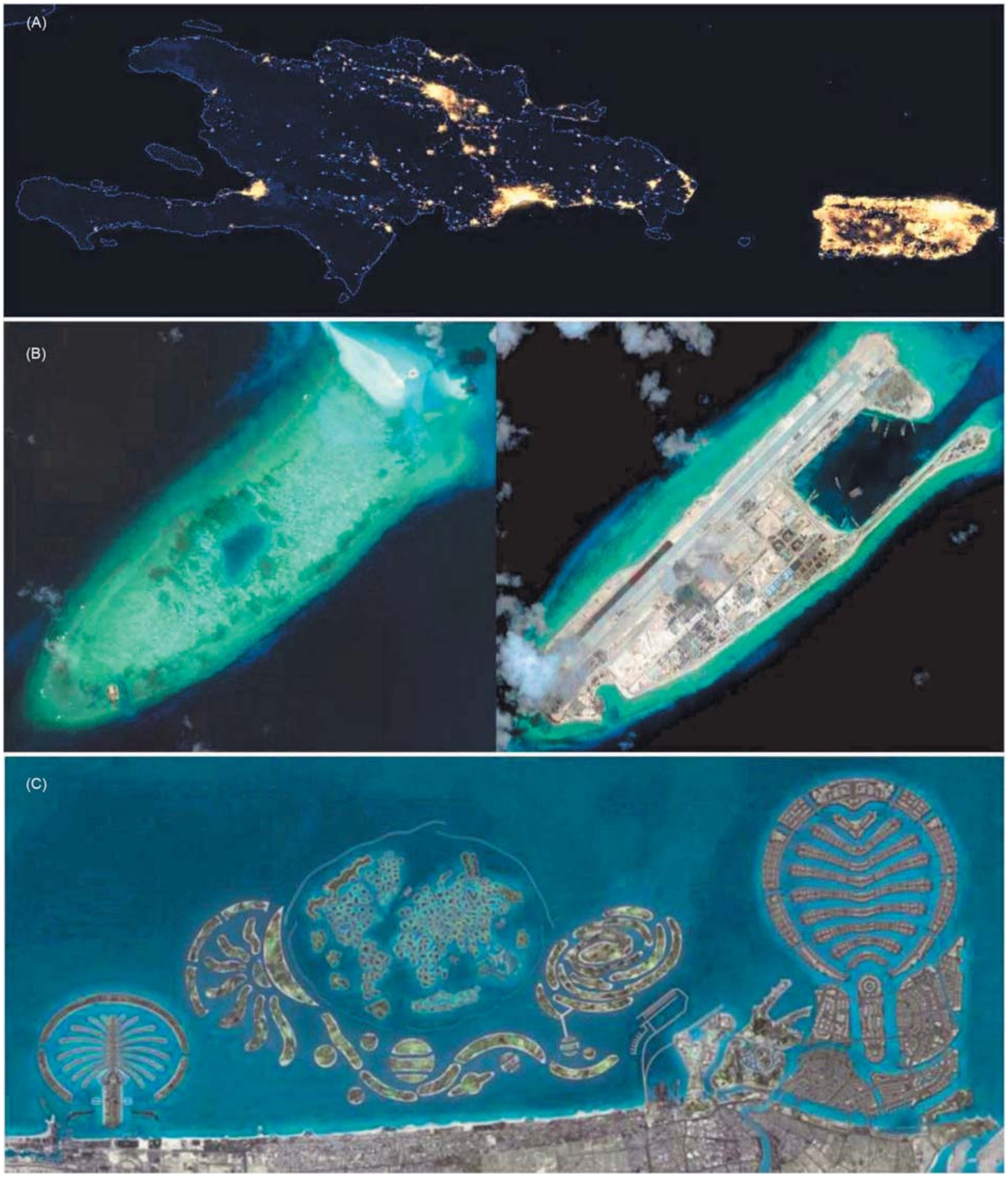

Fig. 1 Islands in the Anthropocene. (A) Continental islands of Hispaniola and Puerto Rico at night. (B) The submerged oceanic island of Fiery Cross reef (永暑礁)in the South China Sea before and after Chinese construction of an artificial island from dredged sand (source: Asia Maritime Transparency Initiative; Walker 2015; Fiery Cross Reef Tracker: https://amti.csis.org/fiery-cross-reef/). (C) Palm Islands of Dubai (جزر النخيل), planned and currently built.

The rates of these three biogeographic processes are affected by island geography. Here, we review only island area and isolation as they are generally considered the most important geographic characteristics that influence island biogeography according to IBT, as well as its extension termed the general dynamic theory of island biogeography that also considers other aspects of geography such as elevation, and how this geography and the three biogeographic processes change over time (Whittaker et al., 2008).

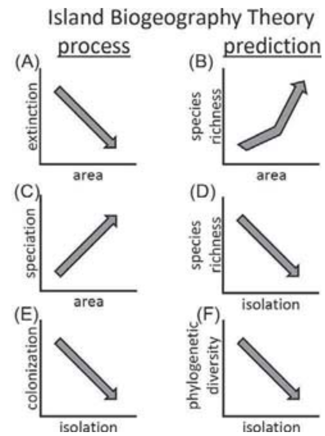

Fig. 2 Major processes and predictions of the theory of island biogeography used to explain variation across islands in the number of species (i.e., species richness) and evolutionary relatedness of species (i.e., phylogenetic diversity). (A) The negative extinction–area relationship predicts (B) a positive species–area relationship (SAR), which may be nonlinear due to (C) the positive speciation–area relationship. (D) The negative species–isolation relationship (SIR) is caused by (E) the negative colonization–isolation relationship that also causes (F) a negative phylogenetic diversity–isolation relationship (PDIR) where the most closely related species are found on the most isolated islands.

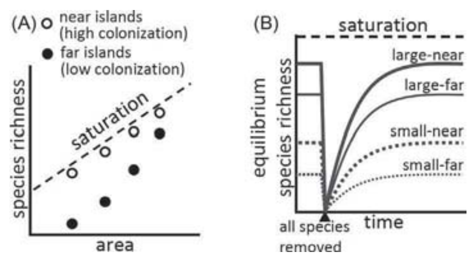

Fig. 3 Tests of island biogeography theory have focused on (A) how islands change when colonization rates change in the Anthropocene (Helmus et al., 2014) and (B) defaunation experiments that suggest that islands have equilibrium species richness values that are determined by how area and isolation influence biogeographic rates (**Fig. 2**).

Islands vary tremendously in area from tiny coral atolls to large continental islands like Hispaniola (**Fig. 1A**). Island area affects speciation and extinction rates whereby larger islands have lower extinction rates and higher speciation rates (**Fig. 2A** and **C**). Larger islands have lower extinction rates because there are more resources and space for populations to grow and expand, making species less prone to going extinct than a smaller population on a small island with fewer resources and space. Larger islands have higher speciation rates because they have more habitat types and geographic space for populations to become isolated and diverge allopatrically. Therefore, a prediction of IBT is a positive and nonlinear species–area relationship (SAR) where larger islands have much higher species richness than smaller islands (**Fig. 2B**).

Island isolation is defined by an island's distance from potential sources of colonists. A typical calculation for isolation is the distance between an island and the nearest equivalent or larger island, continent, or island group, meaning more isolated islands are farther away from other landmasses. The most geographically isolated island in the world is the uninhabited, oceanic, Norwegian island of Bouvet laying ~2600 km southwest of South Africa, while the oceanic island of Tristan da Cunha ~2400 km west of South Africa is the most isolated inhabited island. Island isolation affects colonization rates whereby isolated islands tend to have lower colonization rates than islands closer to other landmasses (**Fig. 2E**). Because over-water colonization can be dangerous, closer islands tend to get more successful colonizations than isolated islands. Therefore, a second prediction of IBT is a negative species–isolation relationship (SIR) where species richness is lower on isolated islands compared to islands close to the continents (**Fig. 2D**). Many taxonomic groups, all with varying overwater colonization abilities, exhibit these SAR and SIR relationships in both tropical and temperate island systems (e.g., plants and birds Blackburn et al., 2016).

According to IBT, island area sets the maximum species richness that an island can contain (**Fig. 3A**). This maximum richness is called a saturation point. Island isolation then determines how close any given island is to its theoretical saturation point, the observed richness at a given point in time is termed *equilibrium species richness*. If the isolation of an island decreases, its colonization rate should increase and thus its species richness would increase to be closer to its saturation point (**Fig. 3A**). Theoretically, a saturation point is only reached when an island is completely unisolated from a continent.

Tests of IBT

IBT provides clear predictions of the species richness of an island based on its area and isolation through the action of colonization, speciation, and extinction (**Fig. 2**). Scientific theories must be rigorously tested; however, rigorous experimental tests of IBT can be challenging due to the size of islands and the scale of the three biogeographic processes involved.

Manipulation experiments to test IBT have largely centered on the defaunation of small islands and recording whether the island returns to its predefaunation species richness. These studies explicitly test the concept of equilibrium species richness (Schoener, 2011). The first, and most well-known experiment, manipulated red mangrove (*Rhizophora mangle*) islands in the Florida keys (Simberloff and Wilson, 1970). Arthropod species richness was first estimated for six islands that varied in area and isolation, but all six were small with low isolation in general (max area, 0.003 ha; max isolation, 1.2 km). Arthropods on the islands were then removed through pesticide fumigation. The researchers surveyed the recolonization of arthropods to the islands and found that the islands recovered to their prefumigation species richness values such that larger islands still had more species than smaller islands and it took longer for the more isolated islands to return to their predefaunation species richness, providing support for equilibrium species richness determined by area and isolation as predicted by IBT (**Fig. 3B**). Other well-known tests of IBT have measured the colonization of species (e.g., spiders, plants, lizards) to islands following a major natural disturbance like a volcano or hurricane that removed existing species. In addition to island manipulations, other tests have used surveys through time to show that even though the identities of species may change on islands, the species richness of islands can be quite stable providing additional support for the concept of equilibrium species richness (Schoener, 2011).

However, the equilibrium species richness levels of islands may be changing in the Anthropocene. Other surveys of islands have not found stable equilibrium species richness values and have attributed this instability to climate change. For example, surveys of plant species richness on Bahamian islands in the 1990s and 2000s found that in the first decade of surveys, species richness was somewhat stable, but in the latter decade extinction rates greatly increased causing species richness to decline (Morrison, 2010). This change in species richness coincided with temperature warming and decreased rainfall across the region.

Anoles in the Anthropocene

While an increase in extinction rates has been well documented in the Anthropocene, another biogeographic process that affects equilibrium species richness, colonization, is also increasing. Through human activities, species are being translocated to new locations across the globe far from their native ranges. The rate at which these exotic species are moved by humans now greatly exceeds the rate of natural colonization historically responsible for introducing species to new locations. In fact, for some species groups, the number of exotic species colonizing an island is much greater than the number of native species going extinct; thus species richness is increasing beyond the natural equilibrium richness level for these groups (Sax and Gaines, 2002). This increase in colonization rate relative to extinction and speciation rate has been used as a way to test IBT in the Anthropocene.

A broad-scale test of IBT in the Anthropocene focused on anole lizards (*Anolis* genus; **Fig. 4**) from the Caribbean islands (Helmus et al., 2014). In the past, Caribbean islands contained endemic anole species where each island had its own species that was not found anywhere else. This is because in the past natural colonization rates to islands were low; long-distance overseas travel across the deep channels that separate the islands is dangerous for an anole, and surviving the journey was relatively rare (e.g., compared to birds) especially to the most isolated islands. On small islands, speciation resulted in just one new species distinct from the ancestral colonizing anole species, but on the larger islands, speciation resulted in multiple new species all descended from the common colonist ancestor (Helmus and Ives, 2012; Losos and Schluter, 2000).

This high endemism has now made it particularly easy to identify exotic anoles that have been translocated to new islands. Today at least 38 populations of 22 anole species have colonized and established on a new island (Helmus et al., 2016). This is in stark

Fig. 4 A male striped anole (*Anolis lineatus*) from Curaçao Island. Photo Credit: M.R. Helmus.

contrast to the one anole species (*A. roosevelti*) that may have gone extinct. It is clear that the colonization rate has increased greatly compared to the extinction rate for Caribbean anoles. We use anoles as an example of how biogeography is changing in the Anthropocene in the following sections.

Islands Are Becoming More Saturated in the Anthropocene

Imagine you and 10,000 other people travel to a city to participate in a week-long research conference. Of course, you and all of these people will need hotel rooms to sleep in. It is easy to envision that the hotels that can accommodate the most people from the conference are the ones that have the most vacancies. A hotel that is completely booked—that is, at its saturation point—can only accommodate a conference-goer by kicking out another guest from a room.

This hotel analogy applies to the exotic anoles in the Caribbean—the islands that are the farthest from their saturation points can accommodate the most exotic species. In other words, IBT predicts that when the colonization rate rises relative to the extinction rate, the islands that are the farthest from their saturation points should have the largest increase in species richness (**Fig. 3A**). Isolation influences an island's equilibrium species richness at a given point in time such that islands that are more isolated for their area should be farther from their saturation point (section "**Species Richness = Colonization + Speciation − Extinction**"). Therefore, in the Anthropocene, the prediction is that there should be higher exotic species richness on islands that are more isolated given their area. Helmus et al. (2014) confirmed this prediction and showed that the least saturated islands are the ones that received the most exotic anoles (**Fig. 5**). This pattern where exotic richness is highest on the least saturated islands also occurs for freshwater Poeciliidae fish in the Caribbean (Furness et al., 2016); however, other studies have found no relationship between geographic isolation and exotic richness (e.g., Blackburn et al., 2016).

Evolutionary History Is Being Obscured in the Anthropocene

The effect of isolation on colonization and area on speciation created measurable evolutionary-biogeographic patterns in Caribbean anole biodiversity. In the Anthropocene, the ancient signal of natural evolution is eroding.

In the past, the effect of island isolation on natural colonization rates has created a phylogenetic pattern with respect to the anole species on islands. Because more isolated islands have lower colonization rates, they tend to have native species evolved from just a few colonizations of ancestors. In contrast, less-isolated islands tend to contain native species evolved from multiple colonizations from different sources. This effect of isolation on the colonization of ancestors to islands results in negative phylogenetic diversity–isolation relationships (PDIRs) where isolated islands contain closely related species, and as island isolation decreases across islands, species are more distantly related (**Fig. 2F**). If colonization rate increases, IBT predicts the negative PDIR should weaken. Caribbean anoles once exhibited a strong PDIR, but that negative relationship of phylogenetic diversity and isolation has been eliminated as predicted (Helmus et al., 2014; **Fig. 6**).

In general, speciation rates are much higher on larger islands than smaller islands (section "**Species Richness = Colonization + Speciation − Extinction**"). This process causes nonlinear SARs where species richness rises slowly for

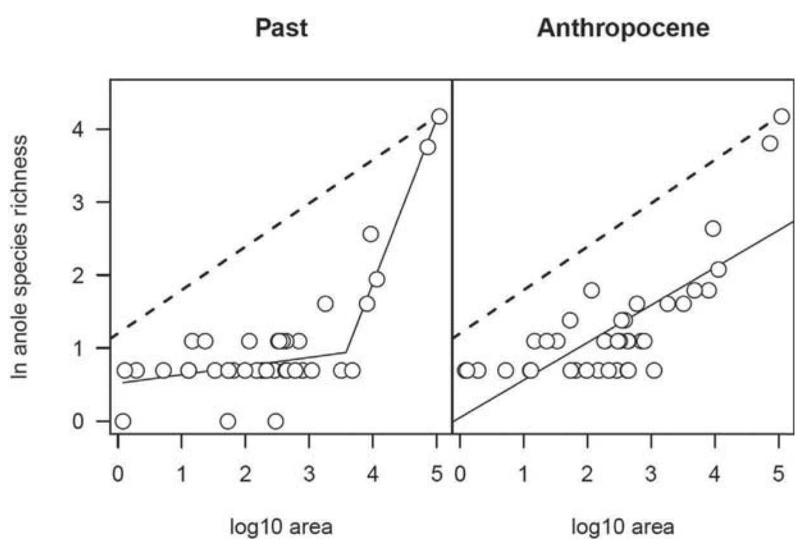

Fig. 5 The Caribbean anole SAR has changed in the Anthropocene. In the past, the SAR was nonlinear (*solid line*) and below the estimated saturation curve (*dashed line*, Helmus et al., 2014) with larger islands having many more species because of high speciation rates compared to smaller islands. In the Anthropocene, the SAR is linear with those islands furthest from saturation (i.e., those furthest from the *dashed line* in the past) having gained the most exotic species.

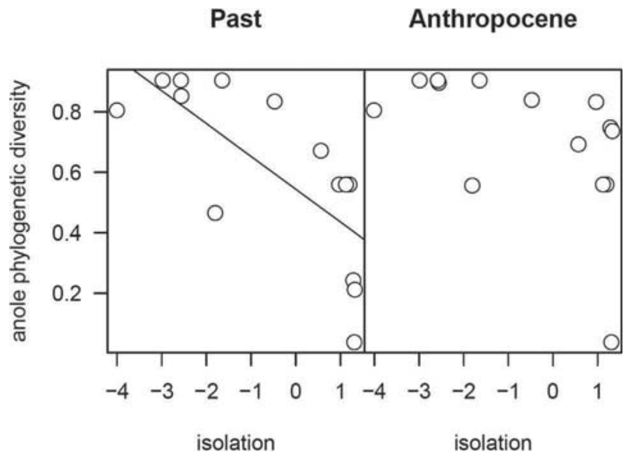

Fig. 6 Anole phylogenetic diversity no longer correlates to isolation in the Anthropocene. In the past, the most isolated islands had the most closely related species due to low colonization rates to those islands. In the Anthropocene, the most isolated islands have gained the most exotics and eliminated the phylogenetic diversity–isolation relationship (Helmus et al., 2014).

smaller islands with low speciation rates and then increases strongly for the largest islands with high speciation rates (**Fig. 2B**). In the past, Caribbean anole species exhibited this two-part SAR across islands (**Fig. 5**). Today, the anole SAR no longer exhibits this two-part relationship; it is linear because many of the islands with low speciation rates have gained the most exotic species (Helmus et al., 2014). This linearization of an SAR due to the spread of exotic species has also occurred for the freshwater Poeciliidae fish of the Caribbean that have been introduced widely via the aquarium pet trade and for biocontrol of mosquitoes (Furness et al., 2016).

Area and Economic Isolation Dominate Biogeography in the Anthropocene

As colonization rate increases, IBT predicts that it is those islands depauperate in species that should gain the most species and approach their area-set saturation points (section "**Islands Are Becoming More Saturated in the Anthropocene**," **Fig. 3A**). As a result of islands gaining species in this manner, the SAR should increase in strength. This is the pattern that has been observed in Caribbean anoles; the anole SAR has increased in strength by ~30% (Helmus et al., 2014).

Comparatively, the SIR should weaken because the islands gaining the most species are those furthest from saturation due to their isolation. Again this pattern was observed in Caribbean anoles; the SIR has decreased in strength by ~75% (Helmus et al., 2014). These same two patterns—strengthening of the SAR and weakening of the SIR—has also occurred for Poeciliidae fish of the Caribbean (Furness et al., 2016).

Economic isolation of islands is conceptually similar to geographic isolation and is the degree to which islands are economically connected to other islands and continents via physical movement of products and people (Helmus et al., 2014). Many exotic species hitchhike to new islands on products moved by ships and airplanes. Anoles, for example, are inadvertently transported in live plant shipments used in ornamental home and resort gardens (Helmus et al., 2016). Shipments of lumber and other goods have also inadvertently spread exotic species to islands. Across the Caribbean there is a strong negative relationship between economic isolation, as measured by the number of cargo ships docking on an island, and exotic anole richness (**Fig. 7**). Besides anoles, economic isolation has been found to determine the species richness of exotic reptiles (Ficetola and Padoa-Schioppa, 2009) and freshwater fish (Furness et al., 2016). Human population size also positively explains plant and bird exotic richness of islands (e.g., Blackburn et al., 2016; Pretto et al., 2012). However, islands with more people not only tend to be more connected economically to the rest of the planet, but also create disturbed and novel habitats that increase the probability that exotics will establish and persist.

Anthropocene Island Biogeography

Although the recent increase in anole colonization rates is due to humans rather than natural forces, IBT still predicts which islands should receive the most exotics based on the island's area and isolation. However, isolation needs to be redefined relative to the colonization mode of the anoles: economic trade. In the Anthropocene, the colonization rate is increasing not just for anoles in the Caribbean, but for lots of species in regions across the globe. Some species, such as freshwater fish, exhibit similar patterns as anoles (Furness et al., 2016), whereas other species do not (Blackburn et al., 2016). In the future, it will be the job of Anthropocene island biogeographers to determine how and when the spread of exotic species is predicted by IBT and whether different processes need to be redefined in anthropogenic terms. At present, it is clear that the biogeography of the Anthropocene is in a state of flux and will differ from the natural biogeography of the past.

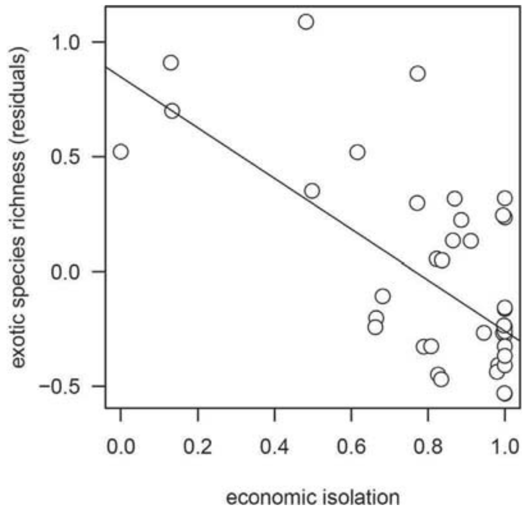

Fig. 7 Exotic anole richness has a negative relationship with Caribbean island economic isolation. Economic isolation was measured by the number of ships docking on islands and the *solid line* depicts a median regression (also see Table 2 in Helmus et al., 2014).

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