Contemporizing island biogeography theory with anthropogenic drivers of species richness

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Abstract

Aim: Island biogeography theory states that species richness increases with habitat diversity and decreases with isolation from source pools. However, ecological theory must incorporate effects of human activity to explain contemporary patterns of biodiversity. We contemporized island biogeography theory by conceptualizing island trajectories of how species richness changes over time with accelerating land development and economic trade, which increase extinction and immigration rates, respectively. With this contemporized theory, we then articulate and empirically assess expected relationships of native, introduced, and total species richness with natural and anthropogenic metrics of habitat diversity and isolation from source pools.

Location: Greater Caribbean region.

Time Period: Database finalized in 2020.

Methods: We built a database of 1042 native and introduced reptiles and amphibians (herps) for 840 Caribbean islands. For each island, we calculated natural and anthropogenic metrics of island habitat diversity and isolation from source pools and used linear model averaging to assess the expected relationships under the contemporized theory for 15 major herp clades .

Results: Natural habitat diversity metrics exhibited positive relationships with native and introduced species richness, strengthening total species richness–area relationships across herp clades. Geographic isolation exhibited negative relationships with native and positive relationships with introduced species richness, weakening total species richness–isolation relationships. Economic area, based on developed land, and economic isolation, based on maritime trade, exhibited negative relationships with native species richness, but positive and negative relationships, respectively, with introduced species richness. Total species richness relationships with these two anthropogenic metrics were strongest in clades with many introduced species.

Main Conclusion: A contemporized island biogeographic theory that includes the effects of land development and economic trade on species extinction and immigration explained current Caribbean herp species richness patterns. As human activity continues to accelerate, the contemporized theory we articulate here will increasingly predict island biogeography of the Anthropocene.

Introduction

In island biogeographic theory (IBT), extinction is defined as the loss of species from islands, while immigration is the dispersal of species to islands, and both operate to determine the species richness of islands (MacArthur & Wilson, 1963; Whittaker et al., 2008). Two main island characteristics, habitat diversity, and isolation from source pools of species, determine extinction and immigration rates and thus drive species richness (Valente et al., 2020). While many advancements describing island biogeography have been made over the years to increase the predictive ability of IBT, the relationships of species richness with habitat diversity and isolation have come to the forefront, providing a framework for many other theories related to island biogeography (Losos & Ricklefs, 2009). The most used metrics to represent habitat diversity and isolation are geographic area and isolation, and as such, IBT provides theoretical expectations for how island species richness relates to these characteristics, explaining the ubiquitous positive species–area and negative

species–isolation relationships. MacArthur and Wilson (1967, pg. 8), while initially describing their equilibrium theory of island biogeography (ETIB), intended geographic area as a proxy metric for habitat diversity, such that larger islands have higher habitat diversity, and this higher habitat diversity provides a higher carrying capacity that supports more species (Ricklefs & Lovette, 1999). Still, area does have a causal effect on species richness since larger islands are able to support larger populations reducing the probability species will go extinct (Kadmon & Allouche, 2007; MacArthur & Wilson, 1967). Similarly, geographic isolation was used as a proxy metric for isolation from source species pools, representing natural dispersal pathways from the mainland and larger islands, such that higher geographic isolation results in lower immigration rates (Losos & Ricklefs, 2009; MacArthur & Wilson, 1963; Valente et al., 2020). Therefore, geographically isolated islands are naturally unsaturated with species and below their carrying capacities set by area-defined habitat diversity.

The general dynamic model (GDM; Whittaker et al., 2008) extended ETIB to include how immigration (and colonization with the establishment of species), speciation, and extinction rates change with habitat diversity over the lifetime of oceanic islands (i.e., island geologic ontogeny). The GDM focuses on how two metrics of habitat diversity, geographic area and topographic complexity, vary as oceanic islands —islands formed by volcanic activity—emerge and recede over their lifetimes (Borregaard et al., 2017; Whittaker et al., 2008). Islands accumulate the most species soon after emergence when habitats are unsaturated allowing for new species to immigrate and higher rates of colonization as new species establish (Steinbauer et al., 2013). Immigration then begins to slow as species fill the island reducing the number of new species in the species pool, and *in situ* speciation adds more species filling the available habitat decreasing the establishment of new species. Geographic area and topographic complexity increase along with species richness as islands fully emerge from the ocean (i.e., reach island maturity and largest area). Peak habitat diversity and species richness occurs slightly after island maturity when erosion begins to form valleys causing topographic complexity to be maximum. The increase to this peak habitat diversity represents ample opportunity for species to diversify or sort into available niche space reducing the effect of antagonistic species interactions. As islands recede, the erosion of island area and topographic complexity reduces habitat diversity, increasing the effect of species interactions on the establishment of new species and causes the reduction of population sizes and an increase in the extinction rate (Borregaard et al., 2017; Whittaker et al., 2008). The process described by the GDM is naturally slow, increasing then decreasing species richness over long geologic timescales, but can be seen as analogous to how human activity can influence immigration and extinction on islands.

Today, humans have altered island characteristics than what typically occurs naturally over much shorter timescales than what typically occurs naturally. Humans transport species across geographic boundaries intentionally or unintentionally through trade. As a result, natural patterns of island isolation from source pools have been altered by economic activities, allowing species to immigrate across geographic boundaries from distant locations that are economically connected (Brown et al., 2021; Seebens et al., 2018). This alteration of island isolation has greatly accelerated since the relaxation of trade barriers after WWII and the invention of modern containerization in the 1950s (Hulme, 2009). Economic activities also change habitat diversity on islands through the anthropogenic transformation of natural habitats creating unsaturated anthropogenic habitats (i.e., land development). Land development, also called land transformation (Hooke et al., 2012), is largely thought to increase island extinctions as it intensifies (Wood et al., 2017). However, through species introductions islands can have higher species richness since most islands are not completely developed, native species use anthropogenic habitat (e.g., Jesse et al., 2018), and some extinctions have yet to be realized (Jackson & Sax, 2010). For example, for Caribbean reptiles and amphibians, there have been 41 known extirpation events, with 60 more that are possible extirpation events, and for plants compared to 625 introduction events (data from this study). The higher human-mediated immigration rate of species than the extinction rate of native species has also been observed across islands globally for birds (Li et al., 2020; but see Sayol et al., 2021) and for plants (Sax et al., 2002).

Given the strong influence of human activities on island habitat diversity and isolation from source pools (Storch et al., 2021), IBT may be less effective at predicting contemporary island species richness comprised

of native and introduced species. Here, we contemporize IBT by proposing logical ideas concerning of how two major anthropogenic activities (land development and trade) influence island species richness based on how habitat diversity and isolation from source pools influences immigration and extinction as detailed by the ETIB and GDM (Fig. 1). From this, we provide intuitive relationships between island species richness and natural and anthropogenic island metrics as a framework that any future macroecological study of island theory can use to frame their own work (Fig. 2). These expectations are for native, introduced, and total (summed introduced and native) species richness and include both direction and relative magnitudes. We then tested the expectations we produced from the contemporized IBT with a comprehensive data set we built for Caribbean island herpetofauna (hereafter: 'herp') and found that the expectations were supported across multiple herp clades.

Contemporization of Island Biogeographic Theory

Over the last two centuries, land development and global trade have accelerated, rising slowly until the mid-1900s and then greatly accelerating throughout the contemporary period (i.e., 1950 to present; Fig. 1A). Termed the "Great Acceleration," this phenomenon dates the start of the Anthropocene (Steffen et al., 2015), a proposed geological epoch signified by anthropogenic impact on the Earth's systems (Lewis & Maslin, 2015). Although other human activities have also accelerated, land development and trade directly impact island habitat diversity and isolation from source pools via species introductions, respectively (Storch et al., 2021). The applicability of IBT to explain extant native, introduced, and total contemporary species richness in the Anthropocene requires incorporating the effects of land development and trade on habitat diversity and isolation from source pools, which reflect how humans influence rates of extinction and immigration.

To contemporize IBT, we begin by considering the trajectories of islands experiencing accelerating land development and trade in the context of the ETIB and GDM (Fig. 1). By articulating this contemporized version of IBT (Fig. 1), new expected relationships between species richness and natural and anthropogenic metrics emerge (Fig. 2), that we then assess in the second part of the manuscript for Caribbean herps. The expectations from the contemporization of IBT (Fig. 2) describe the strength and direction of the relationship. These expectations also act as a framework for future work using richness data to assess IBT by categorizing common island characteristics and providing expectations to test (e.g., Blackburn et al., 2016; Helmus et al., 2014; Losos & Ricklefs, 2009; Losos & Schluter, 2000; MacArthur & Wilson, 1963; Moser et al., 2018; Ricklefs & Lovette, 1999; Rojas-Sandoval et al., 2020; Valente et al., 2020).

Our contemporization of IBT makes two assumptions. First, we assume the effect of humans on speciation rate is not relevant to species richness over contemporary timescales. Second, we only provide expectations assuming that immigration through species introductions is greater than native extinction as is observed for many island clades today (see Sax et al., 2002). This assumption that immigration exceeds extinction has little effect on the expectations for extant native and introduced richness but can influence the relative strengths of the relationships. It is most relevant to the expectations for total species richness, which depends on where islands clades are along their contemporary trajectory (Fig. 1B and C). We explore these assumptions in the discussion.

Contemporary Island Trajectories

ETIB assumes equilibria between immigration and extinction, but island richness in the Anthropocene is not at equilibrium due to accelerating rates and amounts of trade and land development (Fig. 1A), which alters immigration and extinction rates. Under ETIB, this acceleration of human activity causes equilibrium points to shift as immigration and extinction rates vary through time. Thus, islands in the Anthropocene should be conceptualized as following a contemporary trajectory that intersects multiple possible equilibrium points as trade and land development vary over time (Fig. 1B). By the mid-1900s, most habitable islands had been colonized by humans (Keegan & Diamond, 1987) and had species introductions due to low levels of trade (natural immigration replaced by low-trade immigration; shift from equilibrium point "a" to "b_1" or "b_2" in Fig. 1B). Some islands had also experienced increased extinction due to resource extraction, overexploitation,

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and other impacts that occur concurrently with land development (natural extinction replaced by low-development extinction, shift from point "a" to "b_1" in Fig. 1B). However, other islands by the mid-1900s had much less land development resulting in the natural extinction rate being largely maintained (shift from point "a" to "b_2" in Fig. 1B). Today, global trade has greatly accelerated, and most islands have undergone at least low levels of land development increasing extinction rate (shift from point "b_1" or "b_2" to "c" in Fig. 1B). In the future, a plausible scenario is that humans will continue to transform island areas, increasing extinction rates of both native and introduce species to cause a decline in the equilibrium species richness compared to today (shift from point "c" to "d" in Fig. 1B). As land development and trade continue to increase in the Anthropocene, the trajectory will go beyond point "d" potentially further lowering the species richness equilibrium until both land development and trade plateau. Under a contemporized IBT, islands are consistently in transition between equilibrium points without reaching them until introduction rate matches extinction rate and richness is at low equilibrium value for those islands with high development and trade (i.e., point d in Fig. 1B). Shifting, never reached equilibria can happen due to natural environmental and geomorphological changes of islands, as described by the GDM (Whittaker et al., 2008, 2017), or through the anthropogenic processes outlined here.

The GDM articulates a natural species richness trajectory of an island that varies in habitat diversity and operates on geologic timescales far greater than the timescales of human activity(Whittaker et al., 2008, 2017). To further contemporize IBT, we articulate an island trajectory based on how land development affects habitat diversity (Fig. 1C), using the GDM as a reference. Species richness first increases and then decreases along a land development ontology (Gainsbury et al., 2022; Marzluff, 2008) similar to how species richness varies under the GDM with the geologic ontology of islands (Whittaker et al., 2008), but this pattern may vary slightly depending on ecological and environmental context (see McKinney, 2008). As development begins, anthropogenic habitat, unsaturated with species, increases habitat diversity (Marzluff, 2008; McKinney, 2002), which is filled by immigrating species introduced via trade. As development continues, anthropogenic habitats become saturated, the accumulation of new species slows since introduced species are less likely to be a new species or to establish due to increased antagonistic interactions with the incumbent community, and native extinction rate increases due to loss of natural habitat. Species interactions are a part, either implicitly or explicitly, of IBT and can influence immigration and extinction rates. For instance, intermediate land development can ameliorate antagonistic interactions between species by separating them in niche space or causing the extinction of ecological enemies allowing for more species to cooccur on an island (Marzluff, 2008) giving rise to peak species richness at intermediate levels of development along the land development ontology (Fig. 1C). Extinction rate is highest and the establishment rate of introduced species lowest once most of the island has been developed giving rise to lower amounts of habitat diversity on the island due to the loss of natural area and the homogenization of habitat associated with high levels of land development (Western, 2001).
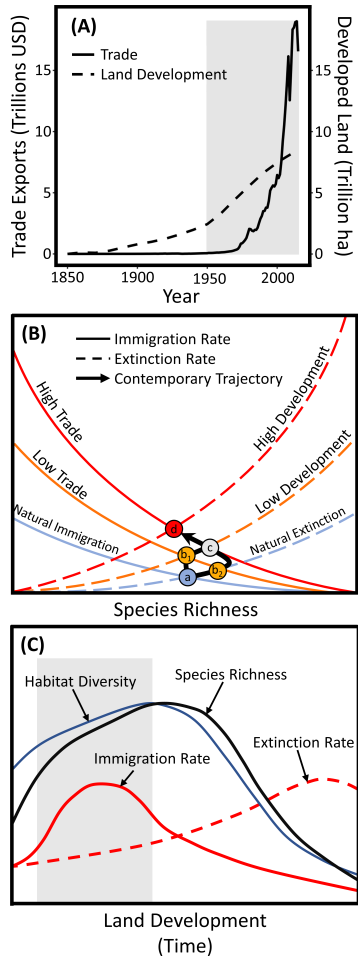
Figure 1: **Figure 1**: Contemporized island biogeography theory (IBT) accounts for (A) global trade and land development, which influence extinction and immigration rates, and has greatly accelerated during the contemporary period (gray shading). (B) Under the equilibrium theory of island biogeography (ETIB), the native species richness of an island is set by an equilibrium between natural immigration and extinction (point a). During the Great Acceleration (A), immigration and extinction change causing the equilibrium to move along a trajectory depending on the relative acceleration of trade vs land development on the island. The black arrow shows an expected trajectory through points "b_1" or "b_2" (pre-acceleration) and "c" (contemporary period) to point "d" (future state), which causes species richness to shift through time. (C) Land development of an island is analogous to the natural ontology of oceanic islands depicted under the General Dynamic Model, an extension of IBT. In the contemporary period (gray shading), development initially increases habitat diversity that allows for an increase in the establishment of introduced species which increases due to increased trade (i.e., increased immigration) and thus causes species richness to rise. As development increases, habitat diversity and the establishment of introduced species decrease while extinction rate increases resulting in decreased species richness. Data plotted in panel A were from United Nations (2011), Federico & Tena-Junguito (2017) and Ellis et al. (2020), panel B was adapted from figures 7-8 in MacArthur & Wilson (1967), and panel C adapted from figure 4 in Whittaker et al. (2008).

Considering the contemporary island trajectories we described above, we next articulate contemporized island biogeographic expectations of the relationships of habitat diversity and isolation from source pools with contemporary species richness (Fig. 2). Categorizing island metrics based on whether they describe

habitat diversity or island isolation allows for expectations to be developed for other metrics common to biogeographic studies and highlights not only the expected relationship of the metric under IBT, but also links to the processes – immigration, extinction and speciation, and their interactions represented by the metric. Note that the contemporary trajectories we conceptualize here do not directly address geographic area as an island characteristic because area is often used as a habitat diversity metric since it allows for a large enough sample of habitats, which more directly control the presences of species (MacArthur & Wilson, 1967; pg. 8). We assume many islands are close to point "c" in Figure 1B. However, these islands are likely not at that equilibrium and are instead in the first half of their land development ontogeny where immigration rate is higher than extinction rate due to increased trade but moderate land development (grayed area in Fig. 1C).

Habitat Diversity Metrics

The most frequently used natural metric of habitat diversity is geographic area, which under IBT decreases extinction rates by supporting more species with larger population sizes (Ricklefs & Lovette, 1999). Immigration is also higher on larger islands, which are bigger targets for dispersing species (Lomolino, 1990). Other common natural metrics of habitat diversity are topographic complexity (Roell et al., 2021); natural area (amount of natural land cover, Rojas-Sandoval et al., 2020); and island spread, since when banks (i.e., groups of historically connected islands) are the unit of analysis, banks with more spatially spread out islands may have more species (Cabral et al., 2014). Geographic area has a well-established relationship with multiple other island characteristics that increase species richness (Ricklefs & Lovette, 1999 and citations within) as well as having its own causal factor increasing species richness (Kadmon & Allouche, 2007), so geographic area relationships with species richness should be stronger than the relationships for the other, more specific, natural habitat diversity metrics. The effect of area can also be dependent on the presence of speciation and overall isolation of the island system (Losos & Parent, 2009). IBT is a neutral theory that assumes native and introduced species are ecologically equivalent. Thus, natural metrics of habitat diversity are expected to correlate positively with native, introduced, and total species richness overall (Fig. 2). However, the strength of the relationships of natural habitat diversity metrics with introduced species richness should be lower than for native species richness because the introduction of species has occurred over a comparatively shorter timescale.

Anthropogenic metrics for habitat diversity must account for the amount of geographic area coopted through land development (i.e., economic area) such as agricultural and urban areas (Rojas-Sandoval et al., 2020). The creation of economic area through land development reduces the amount of habitat available for native species adapted to natural habitats leading to smaller population sizes and increased risk of extinction (Seabloom et al., 2002). Increased economic area also increases the establishment of introduced species because introduced species are often transported and introduced to novel unsaturated anthropogenic habitats (Jesse et al., 2018). Therefore, under IBT, the expected relationships of economic area with extant native species richness and introduced species richness are negative and positive, respectively (Fig. 2). There also should be a weak, positive relationship with total species richness for clades where the positive effect of economic area on the rate of species immigration through anthropogenic introductions is higher than its effect on the native extinction rate of native species (Fig. 2). It is important to note that economic area likely scales with geographic area since larger islands typically have larger human populations, so economic area as a proportion of landcover used for economic purposes may be a better metric to use rather than just total amount of developed area. Further, islands with less topographic complexity will also likely have higher economic area since topographically homogenous areas are often transformed from natural landcover to that used for economic purposes (F. Guo et al., 2018).

Isolation from Source Pools Metrics

The most common natural metric of isolation from source pools is geographic isolation. While there are at

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least 70 metrics of geographic isolation (Weigelt & Kreft, 2013), each assumes to represent natural dispersal pathways such that more geographically isolated islands have lower immigration rates from source pools and are thus unsaturated with native species (MacArthur & Wilson, 1963; Valente et al., 2020). Extinction is also lower on less isolated islands due to the rescue effect, such as the recolonization of Caribbean islands by lizards after hurricanes (Schoener et al., 2001). Since more isolated islands are unsaturated with species, introduced species are more likely to establish after introduction (Moser et al., 2018). As a result, the expected relationships of geographic isolation with extant native and introduced species richness are negative and positive, respectively (Fig 2; Moser et al., 2018). The geographic isolation effect should be stronger on native species richness than for introduced species since introduced species are moved by human activities that circumvent isolating geographic barriers that reduce natural immigration (e.g., oceans). These effects will result in a weaker negative relationship of geographic isolation with total species richness compared to native species richness (Fig. 2).

Anthropogenic metrics for isolation from source pools must account for contemporary dispersal pathways that reflect human economics rather than geography (Capinha et al., 2017; Seebens et al., 2018). Such economic isolation metrics have been based on trade, tourism, and size of an island's economy (e.g., Capinha et al., 2017; Helmus et al., 2014; Rojas-Sandoval et al., 2020). For example, since herps are often introduced through shipping cargo (Kraus, 2009; Perella & Behm, 2020), economic isolation metrics built on shipping can explain introduced herp species richness well (e.g., Helmus et al., 2014). Economic isolation also affects native species richness because introductions can rescue declining native populations (e.g., Richmond et al., 2021). Therefore, under IBT the expected relationships of economic isolation with native, introduced, and thus total species richness are all negative, with the native relationship weaker than the other two relationships (Fig. 2). Economic isolation may also scale with geographic area for the same reasons as economic area. Larger islands tend to have larger human populations, which increases the demand for trade decreasing the islands economic isolation. Additionally, there is likely a relationship between topographic complexity and economic isolation since topographic homogenous areas can easily be transformed to produce goods for trade.

Insights

Contemporizing IBT and articulating expected relationships leads to three insights that speak to broader patterns to be expected as the world continues through the Anthropocene. First, natural and anthropogenic characteristics of islands influence native and introduced species richness in different and sometimes opposing ways. For instance, extant native and introduced species richness should exhibit positive relationships with geographic area and other habitat diversity metrics, but opposing relationships with economic area (i.e., native species richness – negative; introduced species richness – positive). Conversely, native and introduced species richness should exhibit opposing relationships with geographic isolation (i.e., native species richness - negative; introduced species richness - positive), but both should have negative relationships with economic isolation. Second, the applicability or ability to detect the expected relationships depends on how much the immigration rate due to introduced species exceeds the extinction rate. Thus, the expected relationships should be easier to detect in clades of species with more introduced species. Third, as human-mediated species immigration pushes geographically isolated islands towards their carrying capacities, a value that may decrease as land development increases (see Fig. 1C), total species richness should exhibit increasingly stronger relationships with geographic area and weaker relationships with geographic isolation as species introductions increase. We assessed these insights and expectations with the contemporary biogeography of Caribbean herp species.
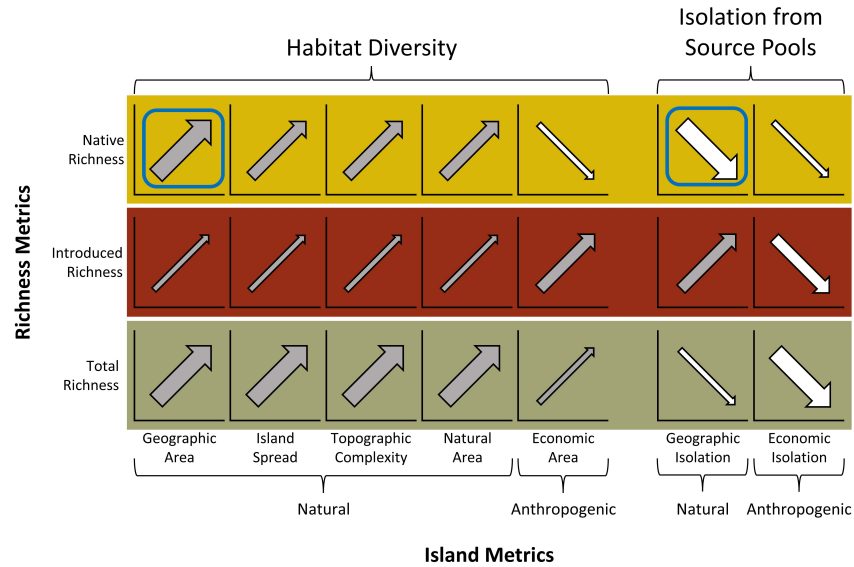
Figure 2: **Figure 2**: Contemporized island biogeography theory (IBT, Fig. 1) provides expectations on the biogeographic relationships of the Anthropocene. Classic IBT provides expected relationships between species richness and two island characteristics—habitat diversity and isolation from source pools (top brackets)—often estimated as relationships of native richness with geographic area and isolation (blue boxes). Today, islands comprise extant native and introduced richness (top two rows), and island characteristics can be estimated with natural and anthropogenic island metrics (bottom brackets). Relationship strength (arrow thickness) and the expectations for total (native + introduced) richness (bottom row) are presented under the assumption that introduced immigration rate exceeds native extinction rate. The metrics (left row and bottom column headings) are not an exhaustive list but are those we calculated for our data set on Caribbean island herpetofauna to test these contemporary expectations (Fig. 4).

Methods

Island Bank System

The Caribbean region spans a broad range of island geographies (Fig. 3B) that have produced both high endemism and the two largest terrestrial vertebrate radiations: the frog genus *Eleutherodactylus* and the lizard genus *Anolis* (Losos & Thorpe, 2004). Within the Caribbean, there are well documented herp distributions (see Supp. Info. Section 1) and phylogeographic reconstructions of ancient dispersal pathways (Glor et al., 2005; Hedges et al., 1992; Tucker et al., 2017). Major human colonization waves occurred ca. 5800-2500 and ca. 1800-500 years ago (Napolitano et al., 2019), followed by European colonization from 1500-1783 (Altman & Horn, 1991). However, most changes to island habitats (Hedges et al., 2018) and species diversity occurred after 1950 (Helmus et al., 2014). Today, herps are frequently introduced to islands (Kraus, 2009; Perella & Behm, 2020) and pervasive deforestation and land development have changed habitat diversity (Hedges 2011). Only 9 of 827 native Caribbean herp species assessed by the IUCN are extinct, but 153 are critically endangered (IUCN, 2021).

We built a database of 840 islands that had herp records (see next section) grouped into 72 banks (Fig. 3A). Banks were based on historical land connections and underwater topography (GEBCO Compilation Group, 2020). We analyzed island banks because natural overwater dispersal within banks is much higher than between banks making banks statistically robust biogeographic units (e.g., Helmus et al., 2014). We included Bermuda in our analysis because it has strong economic ties with Caribbean nations (CARICOM,

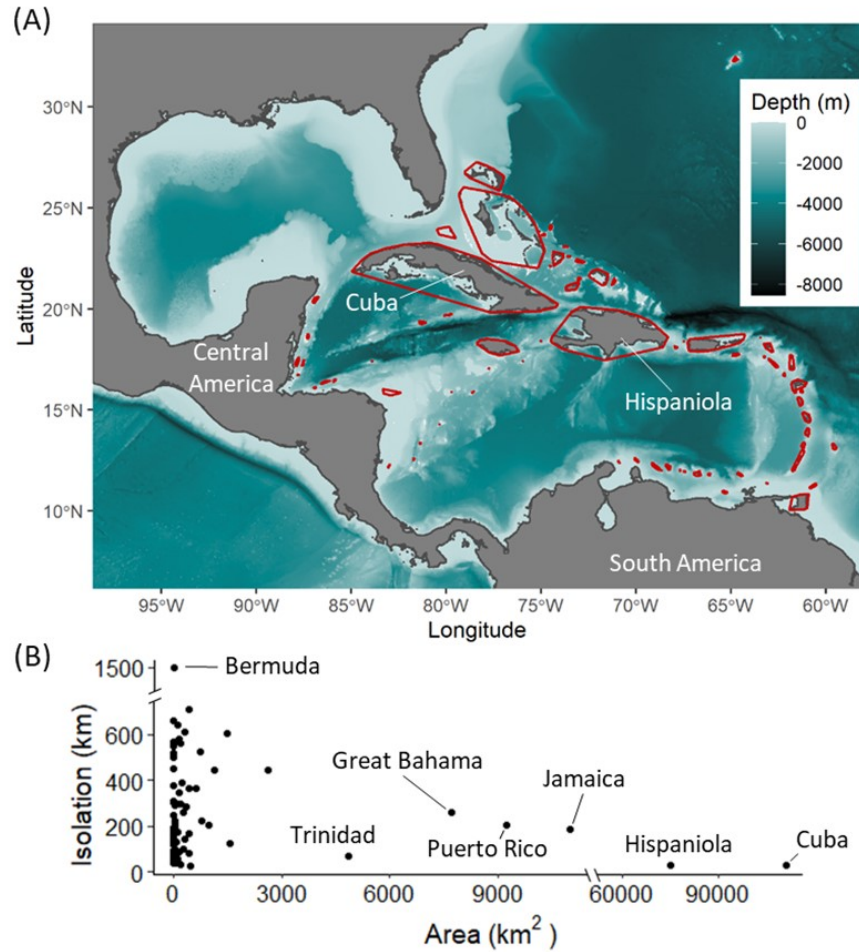2020) and 75% of its herp species occur in the Caribbean

Figure 3: **Figure 3**: The greater Caribbean region (A) includes 78 island banks (red polygons) that exhibit (B) a broad range (note axes breaks) of geographic area and isolation (measured as the minimum distance to any source pool). Source pools for native Caribbean herpetofauna are labeled in white on the map

Island Species Richness Metrics

We performed an extensive literature search of island-level herp records (see Methods Supp. Info. Section 1, searches completed June 2020). Native status was given to extant species indicated in the literature as being native to an island. Introduced status was given to non-native species established on an island indicated from the literature or if a non-native species had multiple records in Global Biodiversity Information Facility (GBIF, 2020), which included data from multiple sources (see Methods Supp. Info. Section 1), that spanned multiple geographic locations and years on an island. While it is possible that some of these species reported in the GBIF records could be rare native species not historically known, given the multiple sources, the extensive research conducted on this system, and the relatively little addition of new native species from GBIF, we believe our native database was complete and this scenario unlikely. We used several sources to standardize species names and taxonomy including caribherp.org (Hedges, 2020), Reptile Database (Uetz et al., 2020), Amphibian Species of the World 6.1 (Frost, 2020), the Integrated Taxonomic Information System

(ITIS, accessed June 2020), and GBIF. Our search yielded 1042 extant species of herps on 72 banks (Table 1).

Different groups of species (i.e., clades) possess varying evolutionary histories and ecologies that can influence biogeographic patterns (e.g., Skeels et al., 2020) potentially leading to differences in the applicability of our contemporary expectations (Fig. 2). Therefore, we inferred the consistency of the expectations across multiple taxonomic clades to understand the generality of the expectations, and how they can be influenced by various historical and ecological contexts. Species were grouped into clades defined by taxonomic class, order, suborder, family, and genus. We identified 154 reptilian and 42 amphibian clades. Native, introduced, and total species richness values per bank per clade were calculated (Appendix 1). Not all clades contained enough species on enough banks to fit robust regressions. Based on a power analysis of the fit of the all-herps model, 15 clades (Table 1) had at least one species on enough banks ([?] 14 banks) to have statistical power of 0.8 (see Methods Supp. Info. Section 2).

Table 1: Eighteen Caribbean amphibian and reptile (herp) clades were used to assess the contemporized IBT expectations (Fig. 2). The dashed line indicates how the data were split for an all-herps analysis and an among-clades analysis among lower rank herp clades (Fig. 4).

Clade	Abbreviation	Taxonomic Rank	Species Richness Native	Introduced*
All Herpetofauna	All	Subphylum	1008	95
Reptilia+	Rept	Class	793	75
Squamata+	Squa	Order	745	64
Amphibia++	Amph	Class	241	20
Neobatrachia++	Neob	Suborder	240	20
Iguania+	Igia	Suborder	244	21
Serpentes+	Serp	Suborder	221	17
Anolis+	Anol	Genus	191	16
Eleutherodactylus++	Eleu	Genus	164	6
Gekkota+	Gekk	Suborder	137	15
Gymnophthalmoidea+	Gymo	Suborder	54	6
Typhlopidae+	Typh	Family	46	3
Hylidae++	Hyli	Family	29	5
Testudines+	Test	Order	18	10
Iguanidae+	Igae	Family	19	4
Cryptodira+	Cryp	Suborder	16	9

* Introduced Species Richness represents the number of species that were introduced to the Caribbean and native Caribbean species introduced to a bank(s) other than their native bank(s).

+ represents clades that are comprised of only Reptiles

++ represents clades that are comprised of only Amphibians

Island Bank Metrics

We calculated four common natural habitat diversity metrics: geographic area, island spread, topographical complexity, and natural area; and one anthropogenic metric: economic area (Table S1). Geographic area was the sum of contemporary land area of each island in each bank from the Global Administrative Areas shapefile (version 3.6, GADM, 2012). Island spread was one minus the total bank land area divided by bank extent estimated as the area of the minimum convex polygon around the islands (Fig. 3A). Topographical complexity was the standard deviation of terrestrial elevation (Amatulli et al., 2018) of each bank from

STRM Digital Elevation Data (90m resolution; version 4, Jarvis *et al.*, 2008). Natural area and economic area (Table S1) were the total proportion of bank area covered by natural or economic land cover types in the Annual International Geosphere-Biosphere Programme classification layer of the MODIS Land Cover Type Yearly Global 500m data (Friedl & Sulla-Menashe, 2015). Natural area included all forest, grassland, wetland, savanna, and shrubland land cover types. Economic area included all cropland and urban land cover types. The "cropland/natural vegetation mosaics" type was split evenly between the two metrics. Bare ground and permanent water cover types were excluded.

We calculated a natural and an anthropogenic metric of source pool isolation: geographic isolation and economic isolation (Table S1). Mainland South and Central America plus the continental islands Cuba and Hispaniola have acted as natural source pools for all Caribbean herps (Ali & Hedges, 2021; Glor et al., 2005; Hedges et al., 1992). We used the minimum distance from the geographic centroid of a bank to the shoreline of the nearest mainland or continental island source (Fig. 3) as geographic isolation (Weigelt & Kreft, 2013; see Methods Supp. Info. Section 3 for comparison to other isolation metrics). We estimated economic isolation from individual ship dockings at ports in the greater Caribbean region in March, June, September, and December of 1979, 1991, 2003, and 2015 for cargo, cruise, and passenger ships (Loyd's, 2020). We took the inverse of one plus the summed total number of ship visits from outside a bank to docks within each bank across all months, years, and ship types as our economic isolation metric.

We included human population density as an eighth island metric (Table S1) as is common for other contemporary studies (e.g., Blackburn et al., 2016; Capinha et al., 2017). Bank population density was estimated as the number of people living on a bank averaged over every five years from 2000 to 2015 (Population Count version 4, CIESIN, 2018) divided by bank area. Under IBT, human population metrics are proxy metrics for the mechanisms by which humans influence species richness—altering habitats for economic gain and moving species via economic connections—which are better represented by explicit metrics. Thus, our expectation for population density is that it will have negligible effects on species richness when economic area and economic isolation are included in the models.

Statistical Analyses

To assess the contemporary expectations (Fig. 2), we regressed native, introduced and total species richness of each bank on the eight bank metrics for all herps combined and each of the 17 clades separately (Table 1). Species richness and bank area were natural log transformed and geographic isolation square root transformed. All variables were standardized by mean centering and dividing by the standard deviation to make coefficients comparable. Models of every predictor combination were fit, the models that accounted for 95% of the cumulative model weight were averaged, and the 95% confidence intervals of the model-averaged coefficients were determined (Burnham & Anderson, 2003). Since collinearity among explanatory variables can create problems when model averaging, we standardized the coefficients of the models to be averaged by their partial standard deviation (Cade, 2015). The contemporary expectations were supported if the direction and relative magnitudes matched, and the 95% confidence interval did not encompass zero. To summarize the relationships across the clades, we calculated coefficient averages and standard errors weighted by the model's Cohen's f^2 (i.e., the effect size for the explanatory power of the model) excluding the all-herp model. These 16 models (all herps + 15 clades) were robust; most pairwise correlations of the predictor variables were less than 0.5, variance inflation factors were less than three (Table S2), all model residuals exhibited low heteroskedasticity, and errors approximated normality (see Methods Supp. Info. Section 4).

All data used in analyses are available in Appendix 1 and Supplemental Information Table S1 and through Dryad (Gleditsch, 2022).

Results

The contemporary expectations (Fig. 2) were supported by our analyses of Caribbean herp island biogeog-

raphy with geographic area and isolation still having strong influence over island species richness (Fig. 4, Table S4). The natural habitat diversity metrics had positive effects, and geographic area consistently had the largest effect compared to all other island metrics for all but the introduced species richness metrics. The positive effects of area on native and introduced species richness combined to produce a stronger, positive effect on total species richness, as total species richness is native plus introduced species richness. Topographic complexity had strong positive effects on native and total species richness, but its effect on introduced species richness was weak which did not strengthen the effect on total species richness like with geographic area. This is likely because the magnitudes of its effect on introduced species richness were more variable among clades than geographic area (Table S4). Similarly, island spread and natural area had positive effects on all three species richness metrics with the strongest effect being natural area on introduced species richness, but these effects were relatively weak and inconsistent among clades. For geographic isolation, as expected there were generally strong negative native species richness relationships, strong positive introduced species relationships, and the species–isolation relationships for total species richness were negative but weaker than native species richness (Fig. 4, Table S4).

Economic area and economic isolation both explained total species richness as expected, but their effects were weaker than geographic area and isolation (Fig. 4, Table S4). Economic area had consistently strong positive effects on introduced species richness, weak negative effects on native species richness, and little effect on total species richness. Economic isolation had strong negative effects on introduced species richness, weaker negative effects on total species richness, and even weaker negative effects on native species richness. Human population density was a poor explanatory metric of contemporary species richness compared to economic area and isolation (Fig. 4, Table S4).
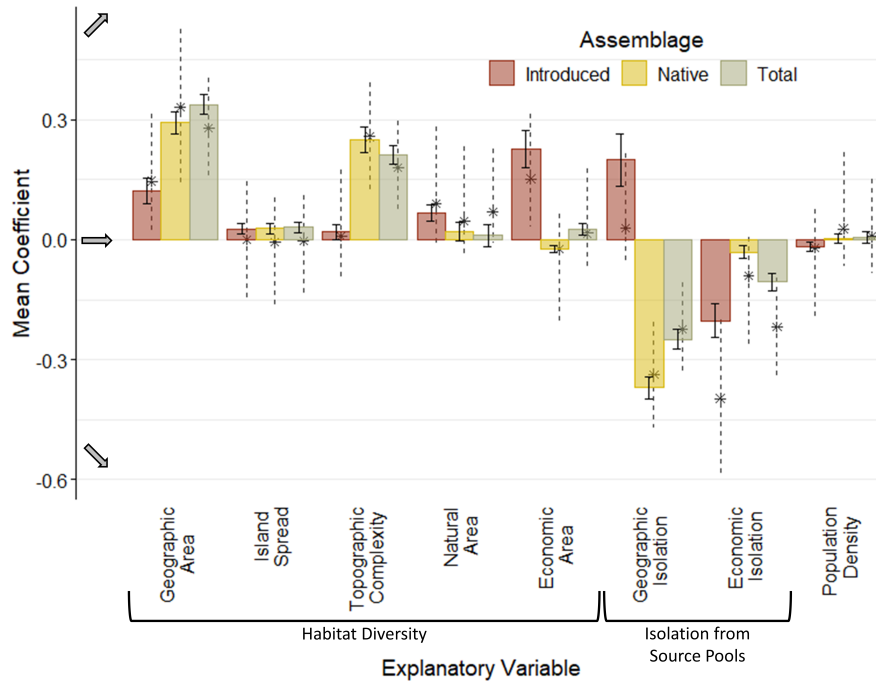
Figure 4: **Figure 4**: General patterns of the contemporary species richness relationships observed for Caribbean island herpetofauna were as expected under the contemporized island biogeography theory (Fig. 2). Bars are the weighted mean of model-averaged coefficients of 15 clades (Table 1) with error bars representing the weighted standard errors to represent a summary of the cross-clade consistency of the relationships. Gray asterisks are model-averaged coefficients for the all herps analysis (Table 1) with dashed 95% confidence interval error bars (Table S3). Gray arrows along the y-axis represent the direction of the relationship given by the mean coefficient for comparison with the expectations in Fig. 2.

Across clades, the strongest, consistent relationships observed were the classic species–area and –isolation relationships with native species richness (Fig 4). Geographic area positively affected native species richness for all but the five least specious clades (Fig. 5A, Table 1), and there were negative species–isolation relationships for all but two clades (Fig. 5E). For introduced species richness, positive geographic isolation relationships were found for three amphibian clades and three reptilian clades (Fig. 5E). For clades with a large proportion of introduced species, there was no effect of geographic isolation on total species richness (Fig. 5E), but the effect of geographic area was still strong (Fig. 5A). For the other natural metrics, topographic complexity had consistently strong positive effects for native and total, but not introduced, species richness (Fig. 5C). Even though there was a positive overall effect of island spread and natural area on species richness (Fig 3), these effects were small across the clades and mostly had confidence intervals encompassing zero (Fig. 5B and D).
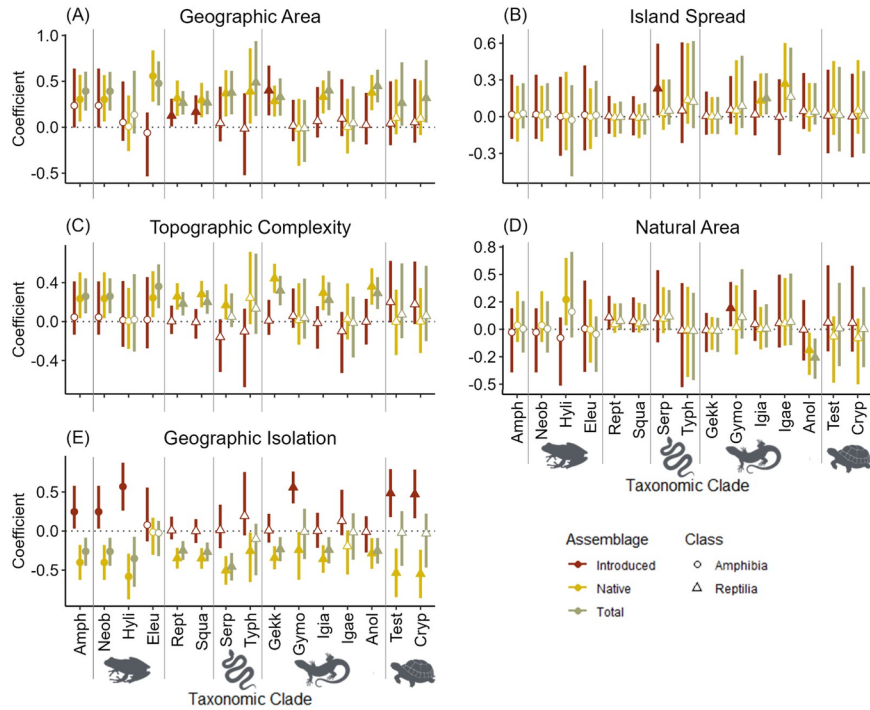
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Figure 5: **Figure 5**: The contemporary framework as it relates to natural island metrics was relatively consistent across taxonomic clades with some variation in select amphibian (circles) and reptilian (triangles) clades. Shown are the model-averaged coefficients for (A) geographic area, (B) island spread, (C) topographical complexity, (D) natural area, and (E) geographic isolation from the averaged multiple regression models of species richness. The introduced, native, and total (red, yellow, and gray, respectively) species assemblages of each clade were modeled separately. Error bars represent the 95% confidence intervals of the model-averaged estimates. Filled points indicate estimates whose confidence intervals do not encompass zero while unfilled points indicate estimates whose confidence intervals encompass zero. Vertical gray lines are grouping the clades into common herpetological groupings (i.e., Frogs, Snake, Lizards, and Turtles; denoted by illustrations along the x-axis). Although, it is important to note that the Neobatrachia (Neob) clade also has toads within it.

Clades with the highest number of introduced species generally exhibited the strongest introduced species richness relationships with economic area and isolation (Fig. 6). Economic area had a positive effect on introduced species richness for seven reptile clades (Fig. 6A) and six of these clades had greater than ten introduced species (Table 1). Economic isolation had negative effects on the introduced species richness of six clades, and all had more than ten introduced species (Fig. 6B) and were among the largest clades in our study (Table 1). Relationships between introduced species richness and the anthropogenic metrics were generally stronger than relationships with native and total species richness. Economic area had very weak negative or no effect on native and total species richness across the clades (Fig. 6A). Economic isolation decreased total species richness for the two largest reptilian clades and Serpentes, and native species richness decreased with increased economic isolation for Squamata (Fig. 6B). Human population density had a strong effect on only two clade assemblages (Fig. 6C).
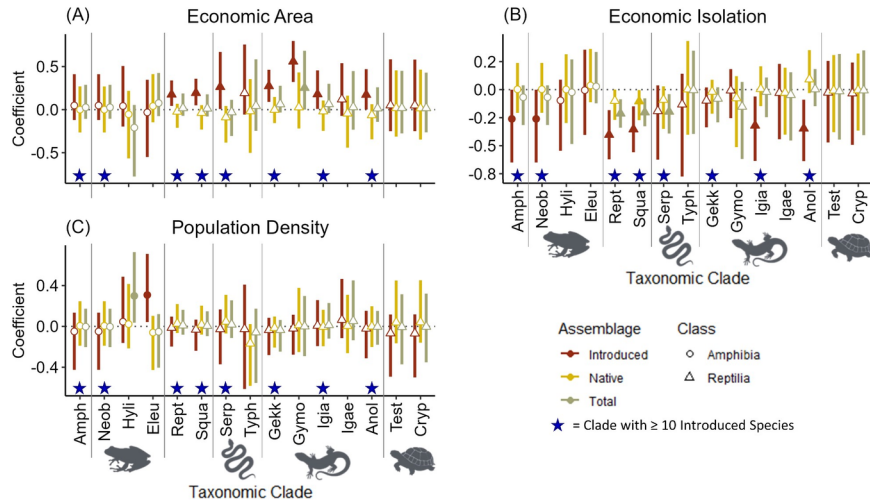
Figure 6: **Figure 6**: The contemporary framework as it relates to anthropogenic island metrics for reptile (triangles) and amphibians (circles) was consistently observed across taxonomic clades with at least ten species introduced outside their native range (blue stars). Shown are the model-averaged coefficients for (A) economic area, (B) economic isolation, (C) population density from the averaged multiple regression models of species richness. The introduced (red), native (yellow), and total (gray) species assemblages of each clade were modeled separately. Error bars represent the 95% confidence intervals of the model-averaged estimates. Filled points indicate estimates whose confidence intervals do not encompass zero while unfilled points indicate estimates whose confidence intervals encompass zero. Vertical gray lines are grouping the clades into common herpetological groupings (i.e., Frogs and Toads, Snake, Lizards, and Turtles; denoted by illustrations along the x-axis).

Discussion

The Anthropocene is defined by the way human activity has impacted natural processes, and classic ecological theory needs to incorporate this activity to explain contemporary biodiversity patterns (Fig. 1). We articulated multiple expectations based on island biogeography theory (IBT) for how natural and anthropogenic metrics of habitat diversity and isolation from source pools influence contemporary species richness (Fig. 2). By categorizing the expectations by what they describe, we provide a framework for future development of expectations for other metrics that describe habitat diversity and isolation and to better link how humans have influenced immigration, extinction, and speciation, as well as their interactions. Our analysis of contemporary Caribbean herp island biogeography (Fig. 3) generally supports the expectations, uncovering, for example, the classic positive species–area and negative species–isolation relationships for native species richness, positive geographic area and isolation relationships for introduced species richness, and matching expected relationships between total (native + introduced) species richness and anthropogenic metrics of economic area and isolation (Fig. 4). With these results, we show how IBT explains contemporary island biogeography when incorporating anthropogenic metrics related to how humans alter habitat diversity and isolation from source pools in lieu of general human-impact metrics such as human population density, which in our analyses had little effect.

As expected, native and introduced Caribbean herp species richness had positive area relationships, while native species richness had negative and introduced species richness had positive relationships with geographic isolation. As a result, total species richness overall had stronger and weaker relationships with geographic area and isolation, respectively, compared to native species richness (Fig. 4). This supports the conclusion that isolated, unsaturated island should accrue the most introduced species (Moser et al., 2018). For five

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clades, introductions have completely nullified any effect of geographic isolation on total richness (Fig. 5E). Thus, if human-mediated immigration of introduced species continues to exceed native species extinction like it currently does for Caribbean herps, we should see an intensifying of the changes in the relationships we observed due to an increasing effect of economic trade on immigration. Specifically, the geographic species–area relationship should become increasingly stronger, and the geographic species–isolation relationship should become increasingly weaker. Interestingly, for some Caribbean herp clades, human-caused extinctions may have reduced native species–area relationships. Native species–area relationships were weak for turtles (i.e., Testudines and Cryptodira) and clades with large-bodied lizards (i.e., Iguanidae and Gymnophthalmoidea). Turtles and large-bodied lizards had many extinctions in the Late Quaternary (Slavenko et al., 2016), which may have caused their native species–area relationships to be reduced as seen for Caribbean bats (Valente et al., 2017). For turtles though, species introductions may be restoring the relationship. Turtles in contrast to the large-bodied lizards have several species introduced to many islands, and as a result, the total species richness area relationship for turtles is strong (Fig. 5).

The effect of topographic complexity on speciation rate is central to GDM (Whittaker et al., 2008), and may reflect aspects of habitat diversity that positively affect extant native species richness more than introduced species richness. Besides geographic area, the natural habitat diversity metric with the strongest positive effect was topographic complexity, but this effect was much weaker for introduced than native Caribbean herp species richness (Figs. 3, 4). Topographic complexity promotes native species diversity in a number of systems (Badgley et al., 2017; Roell et al., 2021) and may provide refugia from anthropogenic disturbance decreasing native extinction rate. In contrast, a strong relationship with introduced species richness may not be expected as we proposed (Fig. 2) because humans often perform economic activities that create anthropogenic habitat in topographically homogeneous lowland areas (F. Guo et al., 2018). Habitat diversity metrics based on area, particularly economic area, should better reflect the amount of habitat used by introduced species, such as anthropogenic habitat, that exists compared to metrics based on topographic complexity. Indeed, we found a strong positive relationship between economic area and introduced richness overall (Fig. 4) driven by those clades with the most introduced species (Fig. 6A). Thus, topographic complexity should show a much stronger relationship with native species richness, and economic area should explain introduced species richness more than topographic complexity. Importantly, when determining metrics for island biogeographic analyses care should be taken to select variables that have meaningful ecological interpretations and to limit multicollinearity in models. This is important to ensure that the anthropogenic effects on species richness can be determined without being confounded by natural metrics that also influence human activities. More work is needed to understand the contemporary expectations of various natural and anthropogenic habitat diversity metrics and define new metrics. For example, ever increasing global technological capabilities have given rise to high-resolution remote sensing data that can be used to better delineate habitat types, measure productivity, and model vegetation-based habitat diversity and species distributions (Randin et al., 2020).

Economic isolation is now an important driver of contemporary island biogeography. Overall, economic isolation had strong negative relationships with introduced Caribbean herp species richness and weaker negative relationships with native and total species richness (Fig. 4) as expected (Fig. 2); and across clades, the strength of the negative relationships was dependent on the number of introduced species per clade (Table 1, Fig. 6B). However, economic isolation for some clades and islands species groups may be idiosyncratic and based on historical context such as past pet trade or cultural practices (e.g., Agoramoorthy & Hsu, 2007; García-Díaz et al., 2015), which is even more critical for dispersal limited species (Gertzen et al., 2008; Magellan, 2019) and calls for alternate measures of economic isolation. Predictive models of how non-native species are introduced have been developed using trade networks (e.g., Seebens et al., 2016), and these same trade networks can be used to develop economic isolation metrics based on network theory.

The cultural history of a region can influence the biogeographic patterns observed in the contemporary time period (Valente et al., 2017). Even though most introduction events have occurred since the 1950s (Fig. 7), there were still introductions before the 1950s. Though information is lacking about introductions prior to European settlement, early in the European history before the peak of the slave trade between 1750-1800,

introductions in the Caribbean accumulated approximately one species every fifty years (0.02 sp/yr) and this rate increased with the slave trade (0.38 sp/yr) and the increasing connectivity of the islands with the movement of freed slaves (early 1800s; rate during = 0.16 sp/yr), the creation of trade connections with Asia through the Panama railroad and canal (year 1914; rate during period = 0.55 sp/yr). One particular case that is important for the current study is that of the widespread gecko, *Hemidactylus mabouia*, which is thought to have been introduced during the slave trade (Perella & Behm, 2020). However, the contemporary rate is between 2.1 and 11.0 sp/yr and the rate at which *H. mabouia* has been introduced has also increased substantially (Perella & Behm, 2020). Thus, while it is possible that introduction events prior to the 1950s can influence a clades' relationship with our economic isolation, this influence is likely minimal compared to the effect of contemporary introductions. It is the increasing effect of human activity on immigration and extinction (Fig. 1 and 7) that necessitates the use of contemporary island trajectories for understanding island biogeographic patterns in the Anthropocene.
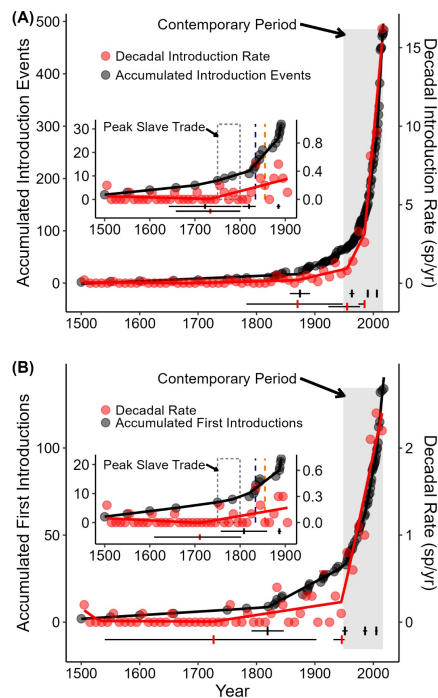

Figure 7: **Figure 7**: The acceleration of species introductions in the Caribbean. (A) The accumulative number of introduction events (black points and black line; left y-axis) and the decadal introduction rate (red points fitted and red line; right y-axis) as determined by dividing the number of introduction events that occurred in a decade by ten years is shown from 1500 through 2018. (B) The accumulative number of species that have been introduced outside their native range for the first time (black points and black line; left y-axis) and the decadal rate of the first introduction of species (red points and red line; right y-axis). The shaded box denotes the contemporary period that is of focus for this study. Insets in both A and B show the relationships before the year 1900 and the period of peak slave trade (1750-1800, dotted box), slave emancipation (1834, blue dashed line), and the creation of the Panama Railroad (1855, orange dashed line). Along the x-axes are the estimated break points (with 95% confidence intervals) from a segmented regression for both the accumulated events (black) and decadal rate (red).

We limited our analyses to clades of herps of the greater Caribbean where we calculated island biogeographic relationships in two separate analyses (Fig. 4): analyses on all Caribbean herp species (our all-herps analysis) and analyses among clades of those species (our 15 clade analyses). This approach is more powerful at

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finding general patterns than analyses focused on only a single clade (e.g., Helmus et al. 2014). A caveat to our comprehensive approach is that the clades we analyzed do not allow for completely independent tests. Clades were not phylogenetically independent and varied in species overlap. Presently, macroecologists lack robust statistical methods to look at biogeographic patterns across nested clades at varying phylogenetic extents, and therefore, new statistical methods are needed to account for the phylogenetically nested structure when testing contemporary IBT relationships and how they change across evolutionary and historic timescales (see Graham et al., 2018). Additionally, further research is needed to determine if theorized relationships (Fig. 2) hold for other groups of species in various archipelagos with varying geographic contexts. Research into the specific relationships between diversity and anthropogenic factors and their form (e.g., linear, nonlinear, log-linear) is also needed to understand the mechanisms that produce them, how they change along an island's trajectory, and how they influence the observed natural relationships. For example, the log-log species-area relationship for Caribbean *Anolis* lizards is now more linear than it once was due to the anthropogenic introduction of species increasing island saturation (Helmus et al., 2014). Additionally, it has been observed that for highly isolated archipelagos, species-area relationships are often steeper than for less isolated archipelagos (Triantis et al., 2012), and now with introduced species these archipelagos may be less isolated leading to shallower relationships (Q. Guo et al., 2021).

We have articulated the most common expected contemporary IBT relationships for extant native, introduced, and total richness, but more work is needed to develop expectations for genetic and functional diversity and extinct species richness. Genetic variation may increase with intermediate levels of human activity on islands due to admixture during species introductions (Kolbe et al., 2008). Additionally, functional diversity may also increase with intermediate human activity due to anthropogenic evolutionary pressures on species leading to phenotypic shifts and potentially speciation (Littleford-Colquhoun et al., 2017; Thomas, 2015; Thompson et al., 2018). The contemporization of island biogeography theory will greatly benefit from the inclusion of data on species interactions to better understand the role niche-based diversification, adaptation, and coexistence play in determining patterns of diversity in the context of anthropogenic impacts. Extirpations and extinctions are an increasingly common result of anthropogenic activity. In the Caribbean herp systems we studied, known extirpations and extinctions are rare, but are likely to increase. While extirpations and extinctions are often poorly documented on islands, especially in premodern times, the impact of past human activity may still be apparent in contemporary estimates of biodiversity (Valente et al., 2017). Although more research into the influence the amount of introduced species has on contemporary island biogeographic relationships, the higher number of introduced species in the species composition of clades that we studied caused weaker relationships with natural and stronger relationships with anthropogenic metrics. Therefore, as extinctions continue to increase and species continue to be introduced, we expect increasing rates of turnover in species composition thereby accelerating the replacement of geographic island characteristics with economic characteristics in determining contemporary biogeography. How geographic and economic island characteristics influence species extinctions will be crucial for theorizing how island biogeography will continue to change in the Anthropocene.

Acknowledgments

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