



Understanding the spread and impact of exotic geckos in the greater Caribbean region

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Abstract

Understanding the patterns and drivers of the spread of exotic species is necessary for limiting their distributions and minimizing their impacts on biodiversity. Species that are spread unintentionally versus intentionally present distinct management challenges that must be addressed with unique solutions. We assessed the spread and impact of exotic gecko species in the greater Caribbean region—a taxa and region predicted to be conducive to a high rate of unintentionally spread exotic species. From the literature, we compiled a database of exotic gecko introductions to the greater Caribbean region, recording the year of introduction, introduction pathway, establishment success, habitat use, and ecological impacts. Exotic gecko species introductions have increased exponentially over time and geckos from multiple biogeographic realms are now present in the greater Caribbean region. Species from distant realms were largely introduced intentionally to Florida via the pet trade, whereas Caribbean endemics were mostly introduced to other Caribbean islands through unintentional or unknown pathways. Regardless of the introduction pathway, most introductions resulted in established populations, usually in anthropogenic habitat. Furthermore, the exotics, *Hemidactylus mabouia* and *H. frenatus*, appear to be on the ‘winning’ end of most species interactions, including those with other exotics. Overall, our results show exotic geckos are spreading both unintentionally and intentionally with a strong potential to displace native gecko species and impact ecosystems as generalist predators. As eradication success is usually low, future conservation efforts should focus on elucidating ecological impacts and preventing new introductions through pathway-specific trade policy, financial incentives, and education.

Keywords Gekkota · *Hemidactylus* · Invasion · Invasive species · Species displacement · Species introduction

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Introduction

Although the increasing spread of exotic species globally is a well-documented threat to biodiversity (Gibbons et al. 2000; Early et al. 2016; Doherty et al. 2016), exact drivers and patterns of spread vary across taxa and regions (Saul et al. 2017; Seebens et al. 2017). From a taxonomic perspective, some species groups are frequently spread intentionally for the purposes of food, biocontrol, pet trade, aesthetics, etc. such as fish, birds, and plants, among others (Blackburn et al. 2009; Richardson and Rejmánek 2011; Turbelin et al. 2017; Rahel and Smith 2018; Ribeiro et al. 2019). In comparison, other taxonomic groups are predominantly spread unintentionally by humans as stowaways in cargo including invertebrates, reptiles, and amphibians (Kraus 2009; García-Díaz and Cassey 2014; Chapple et al. 2016; Turbelin et al. 2017; Meurisse et al. 2019). When these species that are spread unintentionally also evade early detection, it provides an opportunity for them to establish, become invasive, and negatively impact biodiversity (Simberloff et al. 2013).

From a regional perspective, areas that have higher trade volume may receive higher numbers of unintentionally spread species (Westphal et al. 2008; Tatem 2009). While these regions may benefit from import inspection policies, their ability to thwart the introduction of exotics may be overwhelmed by the propagule pressure received from their trade partners (Banks et al. 2015). Within these regions, localities with trade partners that have a lot of exotic species or species with the potential to become exotic, may themselves become inundated with exotic species (Floerl et al. 2009; Hulme 2015). Therefore, in regions where the unintentional spread of exotic species is prolific, identifying the drivers and patterns of exotic spread is a conservation imperative.

The greater Caribbean region is emblematic of the conditions conducive to a high rate of unintentional spread of exotic species. Over the past century, trade among localities within the Caribbean and with outside partners has increased substantially (FAOSTAT 2019). Many Caribbean island nations have asymmetrical trade, whereby their imports greatly exceed their exports, largely to support their booming tourism industries (Timms 2008). On average Caribbean island nations have limited resources for inspecting cargo, and many have strong trade connections with Florida, a hotbed of exotic species (Krysko et al. 2016), two factors which may allow for increased exotic species introductions. Given its island-based geography, a significant portion of the Caribbean's trade is via shipping. This restricts the type of species that can be introduced to those that can survive potentially unfavorable overseas voyage conditions, such as reptiles.

Taxonomically, the Caribbean islands are a biodiversity hotspot with one of the highest rates of reptile endemism in the world (Myers et al. 2000) and most reptile species are endemic to only a single island or island bank (Hedges 2011; Powell and Henderson 2012). This high level of endemism may provide a high potential for exotic species as any species translocated to a different island will likely be exotic. In addition, island ecosystems may be more susceptible to invasion by exotic species in general (Simberloff 1995; Sax and Gaines 2008). Over the past century, the number of exotic reptile species introduced to locations within the Caribbean region has increased exponentially (Kraus 2009; Powell et al. 2011) including species endemic to the Caribbean and elsewhere. Human-mediated dispersal of exotic reptiles became more frequent when global shipping and economic activity increased dramatically after WWII and then more than doubled after the end of the Cold War (Powell et al. 2011; Helmus et al. 2014).

As a group, however, reptiles are diverse and different clades exhibit different patterns and drivers of spread (Kraus 2009; Bomford et al. 2009). Tropical geckos, lizards of the

infraorder Gekkota, have been referred to as the “archetypal poster children” for exotic species that are spread unintentionally via cargo (Kraus 2009). Gekkonidae is the family with the second most introductions globally, after Emydidae, out of all amphibian and reptile families (Kraus 2009). Five gecko species with exotic ranges in the Caribbean region, *Hemidactylus frenatus*, *H. mabouia*, *H. turcicus*, *Sphaerodactylus argus*, and *Phelsuma dubia* (listed in order of decreasing successfulness), are among the top 20 most successful herpetofaunal species at establishing exotic populations globally (Bomford et al. 2009). While the ecological and economic impacts of these introductions are not well-understood (Bomford et al. 2009; Powell et al. 2011), geckos may use similar introduction pathways as less-conspicuous agricultural pests. Therefore, understanding how exotic geckos are spread may also provide insight into the spread of species that are more difficult to detect.

Despite the high success of exotic geckos globally, their spread to Caribbean islands may be a more recent phenomenon (Hoogmoed et al. 2015; Behm et al. 2019). The patterns and drivers of their spread as a group have not been systematically explored in the greater Caribbean region, including whether their predominant introduction pathway is indeed unintentional spread by humans, and how they are impacting native ecosystems. Currently, there are 106 recognized native gecko species in the Caribbean islands, including 97 Sphaerodactylidae (91 endemic) and nine Phyllodactylidae (all endemic) (Hedges 2018). Given this high endemism of native geckos on Caribbean islands and the high success of exotic geckos globally, it is imperative to assess patterns of exotic gecko spread and their impacts on native species.

To gain a deeper understanding of their spread and impacts, we compiled from the literature a database of exotic gecko introductions to the greater Caribbean region and documented interactions between exotic and resident geckos. We maintain the use of the term *exotic* following Colautti and MacIsaac (2004) to refer to non-native species that have been introduced from another location and which may or may not have a negative impact on the local ecosystem. From this database, we synthesized emergent patterns of introduction pathways, geographic origin, establishment success, and ecological impacts of exotic geckos in the greater Caribbean region. Based on our findings, we discuss management and policy options appropriate for addressing the spread of exotic geckos and other species with similar introduction pathways.

Methods

We mined the literature to create a database of the exotic gecko species introduced to locations within the greater Caribbean region. For our study, the *greater Caribbean region* includes the Caribbean islands plus mainland Florida and the Florida Keys. We include Florida given its close proximity and strong economic ties to Caribbean islands, its well-documented exotic fauna, and its history of being a source of exotic herpetofaunal species to Caribbean islands (Powell 2011; Krysko et al. 2016). We define the *Caribbean islands* following Smith et al. (2005) as the islands of the Greater Antilles, the Lesser Antilles, the Lucayan Archipelago (The Bahamas, Turks and Caicos), and the southern Dutch Antilles (Aruba, Curaçao, Bonaire), plus the Venezuelan islands and Trinidad and Tobago. For clarification, we refer to the ‘greater Caribbean region’ when discussing the results of our study but also refer to the ‘Caribbean islands’ to distinguish phenomena and patterns in our results that do not include

Florida. When referring to results from other work, we use the term ‘the Caribbean’ in the same manner as the authors of the study noting that the exact geographic area encompassed by ‘the Caribbean’ may vary across studies.

As a starting point for our database, we used the island-by-island checklist of species compiled by Powell and Henderson (2012), which provides lists of exotic species that are present on each island. We then searched the literature to add more recent arrivals and compile information associated with each introduction (see below). For our literature search, we proceeded location-by-location (at the island and/or country-level for Caribbean islands, and mainland Florida plus individual keys for Florida), first consulting the relevant chapters from Hailey et al. (2011a, b) and references therein, when available. Then, we conducted wider location-level searches using Web of Science (all databases) and Google Scholar with search terms: ‘location name + each species name’ and ‘location name + exotic OR invas* + gecko’ to find published documentations of exotic gecko introductions. While we did not explicitly conduct searches in foreign languages, foreign language documents were examined and included if they emerged during our searches and contained relevant information. Searches for each location were concluded when no additional literature was recovered. Our criteria for including documents in our database was that they provided any of the information surrounding an exotic gecko introduction listed below.

For each introduction of an exotic gecko species to a location (hereafter referred to as a *record*), we documented from the literature when available: (i) the introduction pathway; (ii) the year of introduction; (iii) the habitat where the exotic is found; (iv) the establishment outcome; and (v) the ecological impact of the exotic on resident species. The introduction pathway describes the method by which the individual arrived at the location. We classified introduction pathways as *unintentional* (e.g. stowaway in shipping cargo), or *intentional* (e.g. the pet trade). The year of introduction refers to the actual year the species was introduced, or the year that the authors of the documentation estimated the species was introduced to the location if the actual year was not known. For articles that documented the habitat the exotic used, we categorized the habitats used as *natural*, *anthropogenic*, or *both*. The establishment outcome indicates the result of each introduction and was categorized as either *established*, meaning that there is a breeding population; *extirpated*, meaning that a breeding population was once established but no longer exists; and *stray*, meaning that one or a few individuals were found but did not become established (also termed *waifs* in the literature). For records where the current population status was not known with certainty, we used the last known certain status, i.e. species with unconfirmed extirpations were noted as *established* and species with unconfirmed establishments were noted as *stray*. In addition to these data gleaned from the literature, we also identified the native geographic ranges of each exotic species in our database broadly by region (e.g., Asia, Middle East, South Pacific).

When documented, we included information regarding the ecological impacts of the exotic gecko species on the residents. However, these reports were limited and often pointed to insufficient data to draw conclusions. Therefore, we conducted an additional literature review for studies documenting the impact of gecko species with exotic populations in the greater Caribbean region on resident species outside the Caribbean. We included only papers that provide observational or experimental data to support an interaction, excluding anecdotal or speculative reports, and we include papers that report interactions between exotics and natives as well as among resident exotics.

Results and discussion

In total, we compiled documentation from 119 studies for 252 records of 39 exotic gecko species, belonging to 13 genera and four families, in the greater Caribbean region (Table S1). We also incorporated 16 studies documenting the impacts of exotic gecko species on resident gecko species globally.

Exotic gecko species introductions have increased exponentially in the greater Caribbean region over the past four centuries (Fig. 1a). This exponential pattern is also exhibited by many vertebrate and invertebrate groups globally (Seebens et al. 2017), including exotic reptiles and amphibians globally (Kraus 2009), reptiles and amphibians in the Caribbean (Powell et al. 2011), and exotic species from the lizard genus *Anolis* which is also quite successful in the Caribbean (Helmus et al. 2014). These exponential increases match general increases in the rates of human economic activity since the beginning of the Industrial Revolution globally (Steffen et al. 2011) and in the Caribbean (Powell et al. 2011).

Introduction pathways of geckos in the greater Caribbean region

Understanding a species' introduction pathway is critical for devising effective prevention and/or management strategies (Simberloff et al. 2005). The majority of research on exotic herpetofauna focuses more on establishment success and spread than the transport or initial introduction stages of a species (Puth and Post 2005; García-Díaz and Cassey 2014). Introduced species are often discovered only after establishment rather than at the point of introduction, making it difficult to determine the introduction pathway with certainty. In total, 163 records (63%) representing 18 species have unknown pathways in our database (Fig. 2a). For the 37% of records with known pathways, including 31 species, we identified

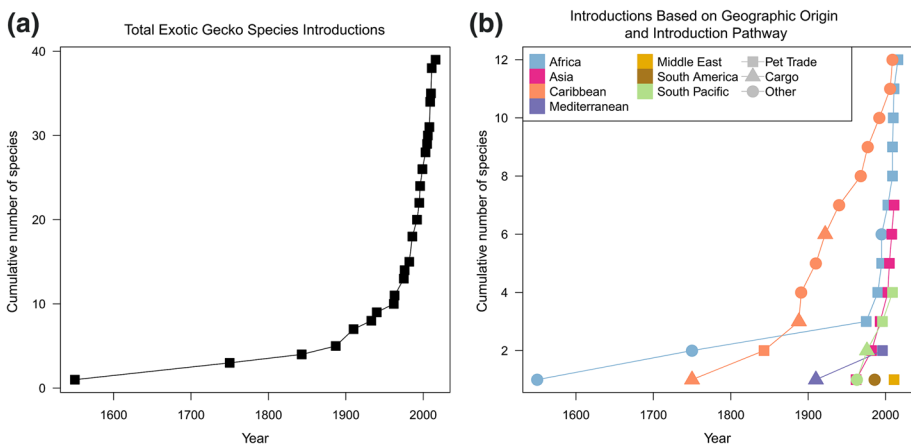


Fig. 1 **a** Cumulative number of exotic gecko species introductions to the greater Caribbean region since the 1500s shown by plotting the earliest year each of the 39 species was documented in a greater Caribbean locality outside of its native range. **b** Same data shown in **a** separated by species' native geographic regions (colors) and designated by introduction pathway (shape). Note these geographic regions do not necessarily indicate the location from which the species was introduced to the greater Caribbean region as many exotic species have multiple exotic populations that could serve as sources for species introduced to Caribbean locations. Color is visible in the online version

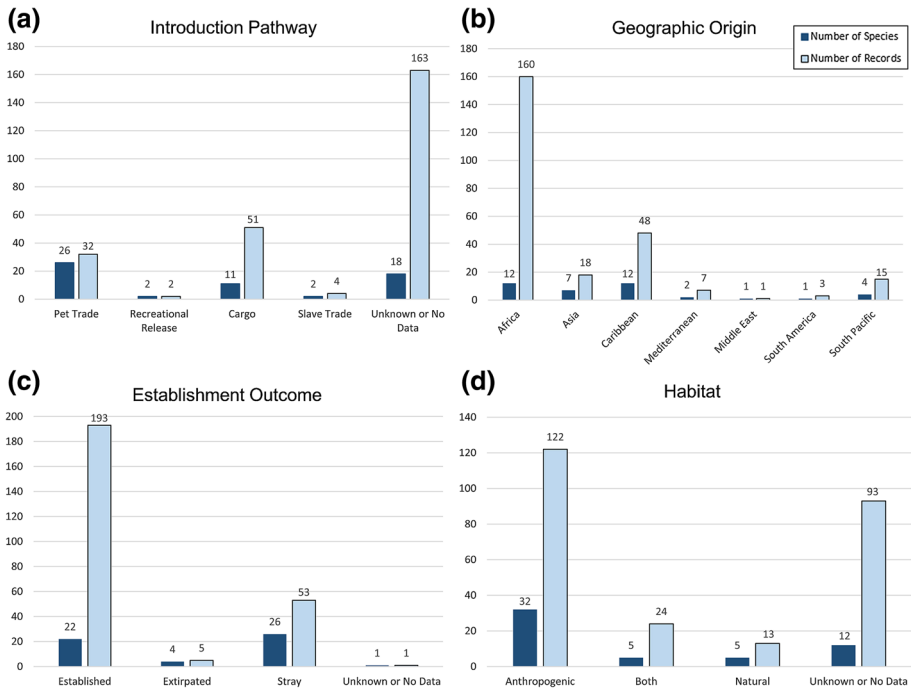


Fig. 2 **a** Introduction pathways that transport exotic gecko species to new locations in the greater Caribbean region; **b** Geographic origin of exotic gecko species introduced to the greater Caribbean region as represented by the geographic region encompassing their native range; **c** Establishment outcomes of exotic gecko species following their introduction to a new location; and **d** Habitat types used by exotic gecko species following their introduction to a new location. Records (light bars) represent all introductions of an exotic gecko species to an island or country; species (dark bars) shows the breakdown of records by species and therefore may be represented in multiple categories in each plot

four pathways of introduction: pet trade (intentional), recreational release (intentional), cargo (passive), and the slave trade (passive). As expected, the most common pathway is via cargo with 51 records (21%) (Fig. 2a). Despite being the dominant introduction pathway in the Caribbean, instances of introduction via cargo are often not well-documented, but species are hypothesized to have arrived with construction materials, shipments of ornamental plants, or as stowaways on recreational ships (Philibosian and Yntema 1976, 1978; Lawson et al. 1991; Rivas et al. 2012; Díaz 2014; Fierro-Cabo and Rentfro 2014; Borroto-Páez et al. 2015). These results are consistent with findings that exotic lizards were spread mostly by cargo globally (Kraus 2009), and that cargo, including the nursery trade (the trade of live plants usually for ornamental purposes), was the pathway responsible for the most herpetofaunal species introductions in the Caribbean (Kraus 2009; Powell et al. 2011).

The other passive introduction category, the slave trade, is attributed to only two species, *Hemidactylus angulatus* and *H. mabouia*, which are thought to have been introduced to the Caribbean region from West Africa (Weiss and Hedges 2007). However, it is difficult to determine exactly which records for specific islands can be attributed to the slave trade and which are a result of possible natural range expansion or subsequent human-mediated transportation after the initial introduction to the Caribbean

region. Therefore, though these species are widespread throughout the region, most of the islands with records for *H. angulatus* and *H. mabouia* do not have known origins or pathways. Only four records, two *H. mabouia* and two *H. angulatus*, documented in the 1930s or earlier from Barbados, Cuba, Hispaniola, and Martinique are proposed to have possibly arrived directly via the slave trade (Grant 1959; Breuil 2011; Fields and Horrocks 2011; Borroto-Páez et al. 2015) (Fig. 2a).

The introduction pathway of *H. palaichthus* on Maria Island, an uninhabited nature reserve in the St. Lucia bank, is uncertain, with support for natural range expansion, human assisted dispersal, and native origins. The species is listed as native in St. Lucia and surrounding islets including Maria Island by Corke (1992), but Powell et al. (2011) report that it is unknown whether the Maria Island population is of natural or anthropogenic origin, and later Powell and Henderson (2012) suggest that the species was introduced by humans, rather than as a result of natural migration.

Among the intentional introduction pathways, the pet trade is the most common pathway with respect to number of records (second to cargo for all types of introductions), and the pathway that has introduced the greatest number of species overall (Fig. 2a). To clarify, we categorize species introduced via the pet trade as *intentional*, because it describes how the species arrived at the location, regardless of whether the species escaped from captivity on its own or was purposefully released into the wild. Certain characteristics of species, such as color pattern, body size, and ease of captive breeding and care determine species' popularity in the pet trade (van Wilgen et al. 2010; Tapley et al. 2011; García-Díaz and Cassey 2014). There are also biological and economic factors that affect the probability of pets being released after purchase, including the adult size and lifespan of a species as well as its rarity and retail price, all of which may influence the cost of care and the value placed on the pet by the owner (Stringham and Lockwood 2018). Pet releases are now a dominant pathway by which exotic species are introduced to new locations globally, and the ecological impacts that many released species pose on native resident species have become a bigger conservation concern (Smith et al. 2009a; Stringham and Lockwood 2018). In the greater Caribbean region, 32 records (12%) of 26 exotic gecko species (67%) were introduced via the pet trade, 31 of which have occurred in southern Florida (King and Krakauer 1966; Meshaka et al. 1994a, b; Krysko et al. 2003, 2010, 2011,.; 2016; Enge et al. 2004; Meshaka et al. 2004; Krysko and Sheehy 2005; Bartlett and Bartlett 2006; Krysko and Borgia 2012; Fedler et al. 2016) and one of which was recently documented in Curaçao (Behm et al. 2019). Many of the releases in Florida are linked to a single property belonging to an animal importer in Broward County (Krysko et al. 2011, 2016).

Two records were categorized as *recreational releases*, which are intentional introductions that are not part of the pet trade, for biocontrol, or for scientific purposes, and include instances where people bring species from their homeland or a place they have visited to their new or current home for aesthetic, acoustic, or sentimental reasons (Kaiser et al. 2002; Kraus 2009). The first is *H. garnotii*, which was established in two disjunct Miami, FL localities in 1964. Both localities were in the immediate vicinity of the homes of University of Miami Institute of Marine Sciences personnel; it is thought that the established populations resulted from "souvenirs" collected during the institute's International Indian Ocean Expedition (1960–1963) as *H. garnotii* is native to the Indo-Pacific (King and Krakauer 1966). Subsequent introductions of *H. garnotii* to Florida have been reported for numerous counties and Everglades National Park, likely introduced through cargo (Wilson and Porras 1983; Krysko et al. 2016). The second recreational release also resulted in establishment and occurred in Martinique in the early 1970s by a rum distillery worker who intentionally

introduced the species, *Gekko gecko*, when he arrived in Martinique from Southeast Asia (Henderson et al. 1993).

The question of *Hemidactylus* introduction pathways

There are several examples of species throughout the Caribbean, such as *Eleutherodactylus johnstonei*, *E. martinicensis*, *Geochelone carbonaria*, and *Iguana iguana*, whose origins, and whether or not they were relocated due to anthropogenic activity, are unknown (Kraus 2009). Similarly, whether *Hemidactylus* originated in the Caribbean islands due to natural over-water dispersal or human-mediated introduction has been a topic of intense debate. Our records include seven species of *Hemidactylus* in the greater Caribbean region, which is the genus with the most records in our database (Fig. S1) as well as one of the most species-rich genera of reptiles globally with about 80 described species (Carranza and Arnold 2006). The vast majority of *Hemidactylus* species have relatively limited native ranges in Africa, Asia, and the Mediterranean, compared to just eight species that are particularly successful colonizers with wide distributions, five of which have global exotic ranges (Carranza and Arnold 2006). The most ubiquitous of the *Hemidactylus* geckos in the greater Caribbean region is *H. mabouia*, with 126 records. Because *H. mabouia* is so widespread and historically reported on many Caribbean islands, there has been debate about whether the species was introduced to the region by humans or via natural over-water dispersal from Africa. Grant (1959) originally reported *H. mabouia* as being introduced from Africa by the slave trade, yet Kluge (1969) presents an argument for natural over-water dispersal and subsequent spread for both *H. mabouia* and *H. brookii* (now *H. angulatus*). While admitting that evidence of anthropogenic trans-Atlantic introduction is stronger for *H. mabouia* than for *H. brookii*, he cites three major arguments in favor of natural dispersal, including being present in the Lesser Antilles very early in the history of the slave trade and at a time when the Lesser Antilles had only recently been settled, that at least some parts of *H. mabouia*'s geographic range in the Caribbean lie outside of usual trade routes and places of human habitation (though there is not an example of this provided), and that they have been recorded from islands that were not major points of entry for slave ships, while also not being recorded from islands that were, such as Jamaica (Kluge 1969).

Opinions shifted again as the use of molecular markers allowed more robust phylogenetic analyses; Carranza and Arnold (2006) used fragments of mitochondrial genes to resolve the genus' ambiguous taxonomy and to try to date the long-distance colonization events. Low genetic diversity was found among 30 specimens of *H. mabouia*, even though they came from 17 localities across a huge multi-continental range spanning Africa, South America, and the Caribbean islands (Carranza and Arnold 2006). This genetic uniformity suggests that colonization of the Caribbean and subsequent spread was recent, as within the last 500 years that humans have been crossing the Atlantic Ocean, rather than ancient over-water dispersal (Carranza and Arnold 2006).

While *H. mabouia* is the most widespread and has arguably the most uncertain origins in the Caribbean islands, the analysis by Carranza and Arnold (2006) was also the first to find genetic and morphological similarities between Cuban samples of *H. haitianus*, thought to be native to the region, and a sample of *H. angulatus* from Equatorial Guinea, suggesting that *H. haitianus* is not a distinct species from *H. angulatus*. Weiss and Hedges (2007) confirm the findings of Carranza and Arnold (2006) that *H. haitianus* is conspecific with African *H. angulatus* and add that the species is likely to have arrived to the Caribbean via slave ships from West Africa. Therefore, any Caribbean records assigned to *H.*

haitianus or *H. brookii* (mentioned above from Kluge 1969) should instead be referred to as *H. angulatus* and not considered native to the region (Carranza and Arnold 2006; Weiss and Hedges 2007). Furthermore, like *H. mabouia*, the genetic uniformity of populations of *H. angulatus* and *H. turcicus* across their exotic ranges imply that colonization and spread from Africa and the Mediterranean, respectively, to the Caribbean was recent (Carranza and Arnold 2006). Despite genetic evidence that these widespread *Hemidactylus* species are recent colonizers, Powell and Henderson (2012) consistently use “I?” in their species lists for *H. mabouia* records on Lesser Antilles islands, meaning it is unclear whether the species was introduced by humans or arrived naturally from Africa or other established populations in the Western Hemisphere (Powell et al. 2011). Overall, it is clear that recent *H. mabouia* introductions (1900s, 2000s) are the result of human-assisted dispersal, but the origin of *H. mabouia* in the Caribbean may never be known for certain.

Geographic patterns

The mixing of species from different biogeographic realms is a hallmark of exotic species spread in the modern era (van Kleunen et al. 2015). To explore patterns of exotic species introductions over time based on geographic origin, we plotted the earliest year each species was documented in the greater Caribbean region based on their native range (Fig. 1b). The oldest record is an African species (*Hemidactylus mabouia*) from the late 1500s, followed by the spread of geckos among Caribbean islands starting in the 1700s. Strong biogeographic mixing did not occur until after 1950 when species native to Asia and the South Pacific were introduced to the greater Caribbean region. A Middle Eastern species, *Eublepharis macularis*, is among the most recent arrivals, not documented in the greater Caribbean region until it was introduced to Florida via the pet trade in 2011 (Krysko et al. 2016).

It is notable that this geographic structuring in the timing of exotic gecko introductions is largely related to the species’ introduction pathways. Most exotic species that are endemic to the Caribbean were introduced as passive cargo or through unknown pathways to other Caribbean island locations. Comparatively, most exotic species with native ranges outside the Caribbean (Africa, South Pacific, Asia) were introduced via the pet trade to Florida. These disparate pathways generate distinct biogeographic mixing patterns in Florida compared to the Caribbean islands, with a more phylogenetically diverse assemblage of geckos in Florida compared to the Caribbean islands. In other species, like grasses, phylogenetic distance is correlated with stronger impacts on the resident community (Strauss et al. 2006; Zheng et al. 2018), yet the implications of these patterns for the impacts of exotic geckos on resident species in the greater Caribbean region is not known.

Almost two-thirds of all exotic gecko species in the greater Caribbean region are native to Africa or the Caribbean, however, the total number of records of species from Africa is over three times greater than Caribbean species due to the highly successful *Hemidactylus* species (Fig. 2b). Given that the exotic geckos in the greater Caribbean region are native to a wide range of biogeographic realms, it follows that suitable climatic conditions may exist in the Caribbean for additional species from these realms that have not yet been introduced. Note, however, that the native geographic range of these species does not indicate the point from which they were introduced to the greater Caribbean region. Many of these species have multiple exotic populations and could have been introduced to the greater Caribbean region from their exotic range. In fact, there is little certainty surrounding the geographic source for these introductions; only three records in our database had confirmed

geographic sources, and they were all intentional introductions. This lack of information on source locations is likely due to the fact that geckos and their eggs are small and likely go undetected when introduced to a new location relative to more noticeable species like snakes (e.g., Perry and Platenberg 2007).

In addition to species' geographic origins, the patterns that emerge from introduction locations may also be useful in predicting and preventing future exotic introductions. The majority of Caribbean countries, islands, or island groups have only one or a few introduced gecko species. Those with more species introductions tend to be more economically connected, such as The Bahamas, which have 14 records representing six species over its nine major islands (Thomas 1968, 1975; Schwartz 1975; MacLean et al. 1977; Franz et al. 1993; Buckner and Franz 1994; Meshaka 1995; Powell et al. 1998; Howard et al. 2001; Hodge et al. 2003, 2011; Lee 2004; Krysko and Borgia 2005; Krysko and Thomas 2007; Henderson and Powell 2009; Knapp et al. 2011; Powell and Henderson 2012; Krysko and MacKenzie-Krysko 2016), or larger islands like Hispaniola, which has four records of four different species (Barbour 1930; Powell et al. 1998; Scantlebury et al. 2010; Powell and Henderson 2012; Borroto-Páez et al. 2015) (Fig. 3a). In Cuba, there are 30 records of introductions representing eight species over its mainland, Isla de la Juventud, and its surrounding cayos (note: only Cayos Coco, Frago, Guajaba, and Romano are visible in Fig. 3) (Barbour 1935; Powell et al. 1998; Martínez Rivera et al. 2003; van Buurt 2005; Carranza and Arnold 2006; Powell and Henderson 2012; Díaz 2014; Borroto-Páez et al. 2015; Alonso Bosch and Borroto Páez 2017). Despite the relatively high number of introductions to Cuba, very few of the introductions occurred in the twentieth century, with no recorded introductions between 1950 and 1999 (Fig. 3b–e). This is likely due to strict economic sanctions against Cuba during this time, which limited opportunities for exotic gecko introductions. Notably, the southern Dutch Antilles islands of Aruba and Curaçao have four and six gecko species introductions, respectively, while Bonaire only has one introduced gecko species (Hummelinck 1940; van Buurt 2005, 2011; Powell et al. 2011; van Buurt and Debrot 2012; Hughes et al. 2015; Behm et al. 2019). Despite being some of the smaller

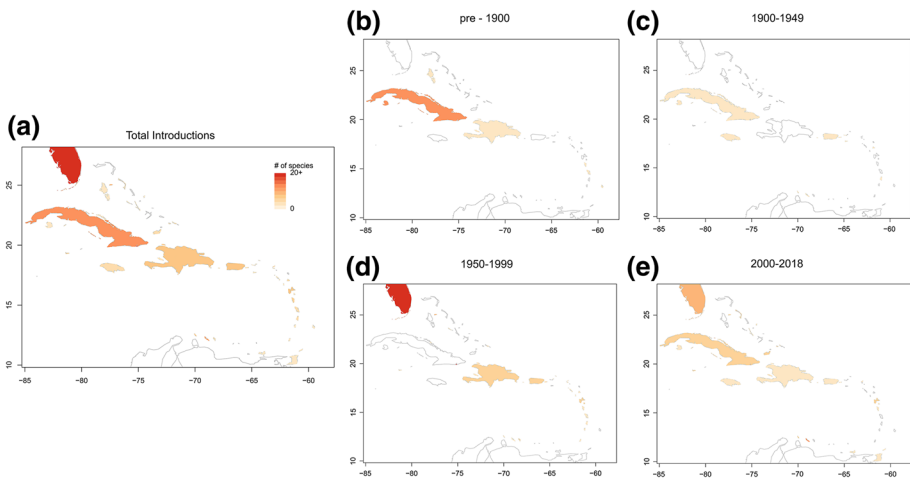


Fig. 3 **a** Total number of exotic gecko species introduced to locations across the greater Caribbean region (Caribbean islands and Florida). Darker shading indicates a higher total number of species introduced. **b–e** Same data mapped in **a** separated to show the number of exotic gecko species introduced to each location across four time periods: **b** pre-1900; **c** 1900–1949; **d** 1950–1999; **e** 2000–2018

islands in the region, Aruba and Curaçao are economically well-connected to the rest of the region, while Bonaire remains largely undeveloped, further supporting that economic connectivity is a driver of exotic spread. These patterns in the Caribbean echo global patterns in which localities that are more economically connected by trade have higher numbers of exotic species across taxa (Westphal et al. 2008; Hulme 2009; Helmus et al. 2014).

In comparison, 60 records of 28 species have been introduced to mainland Florida and the Florida keys (Fig. 3) which can be largely attributed to the pet trade (King and Krakauer 1966; Meshaka et al. 1994a, b; Krysko et al. 2003, 2010, 2011, 2016; Enge et al. 2004; Meshaka et al. 2004; Krysko and Sheehy 2005; Bartlett and Bartlett 2006; Krysko and Borgia 2012; Fedler et al. 2016). However, it appears that the pet trade did not become popular until after 1950, as all 28 species were introduced after that time (Fig. 3b–e).

Establishment success

Although not all exotic species that are introduced to a location establish a population, those that do pose a potential ecological threat to resident species. We found high establishment success: 193 records (77%) consisting of 22 species (56%) resulted in established populations (Fig. 2c). Although lizards have the highest establishment rates of all herpetofaunal groups globally (ca. 38%; Kraus 2009), our estimates greatly exceed these as well as estimates of exotic herpetofaunal species establishment rates in Florida (33%; Krysko et al. 2016) and establishment rates for the Gekkonidae family globally (45%; Kraus 2009). However, our establishment rate is only slightly higher than the establishment rate of all exotic herpetofaunal species in the Caribbean (62.4%; Powell et al. 2011).

Because most of our records have unknown introduction pathways, it is difficult to assess whether particular introduction pathways are associated with a higher likelihood of establishment (Pergl et al. 2017). However, of the established populations with known introduction pathways (53 records), most arrived via passive cargo (62%). Establishment success is often correlated with propagule pressure (Lockwood et al. 2005), and in other systems, such as intentionally introduced passerine birds in New Zealand, low propagule pressure results in low establishment success (Blackburn et al. 2013). Therefore, we expected that gecko species introduced intentionally via the pet trade would generally be strays, as only one or a small number of individuals of a species are transported and are released or escape from their enclosures. Surprisingly, 44% of pet trade records reported established breeding populations. The high establishment success of pet species could be due to their association with humans, as other vertebrate groups, like birds and mammals, with high human association had higher establishment success (Jeschke and Strayer 2006).

The records categorized as extirpated seem to be the result of failed establishment after some initial success rather than intervention by humans to rid the location of an exotic population, as most sources report that the species has not been seen again after the initial documentation (Powell et al. 2011; van Buurt and Debrot 2012). In one case, 40 *Sphaerodactylus mariguanae* were collected in Cockburn Town, Grand Turk by Schwartz in 1968. The species has not been recorded on Grand Turk since, and the removal of 40 individuals from a small founder population could have played a role in its subsequent extirpation (Reynolds and Niemiller 2010; Reynolds 2011). In another case, a localized but thriving population of *Gonatodes albogularis fuscus* existed on Stock Island in the Florida Keys until many of the large ficus trees they inhabited were removed for landscaping (Meshaka et al. 2004).

Establishment success may be related to the types of habitat that exotic species occupy after introduction, as exotic reptiles often do well in anthropogenic or disturbed habitat (Jesse et al. 2018). Also true for other taxa, tolerance of human-impacted habitat was found to be a significant factor in invasion success of freshwater turtles, for example (Masin et al. 2014) and is a major determinant of whether a bird species becomes exotic (Cardador and Blackburn 2019). Edificarian geckos (species that use buildings) and other herpetofauna that are adapted to disturbed habitat may have a similar advantage in initial introduction stages. The majority of exotic gecko species introductions in the Caribbean have occurred near ports and in urban areas; 82% of the species comprising 48% of the total records have been found only in anthropogenic habitat (Fig. 2d). Moreover, 76% of records found in anthropogenic habitat have become established, indicating that many of the introduced species are well-adapted to highly-disturbed habitat. Only 24 records representing five species are found in both anthropogenic and natural habitat (Fig. 2d). There are five species comprising 10 records that were found only in natural habitat in at least one location, though three of these species were found in anthropogenic habitats in other locations: *Gonatodes albogularis fuscus*, *H. garnotii*, and *H. mabouia* (Philibosian and Yntema 1978; Meshaka et al. 2004; Krysko et al. 2010; Daudin and de Silva 2011; Fields and Horrocks 2011). Only two species were found in only natural habitat across all locations: *H. palaichthus* on Maria Island (which may be native, as discussed above) (Corke 1987, 1992; Powell et al. 2011; Powell and Henderson 2012), and *Sphaerodactylus copei cataplexus* in The Bahamas, close to its native Hispaniola (Henderson and Powell 2009).

Ecological impacts

Impacts of exotic geckos on native species in the Caribbean

Despite the high number of introduced gecko species, scant studies have documented the impacts of these exotic geckos on resident gecko species and ecosystems in the greater Caribbean region in a quantitative manner. This low number of studies is particularly concerning given the higher impact of exotic herpetofaunal species on island versus continental ecosystems (Kraus 2015).

Given their ecological similarity to native gecko species, we predict that exotic geckos will have the strongest competitive interactions with native or resident (established exotic) gecko species compared to other native reptile species. We found only one example of a native gecko species that seems to have a competitive advantage over an exotic. In Barbados, the native gecko, *Phyllodactylus pulcher*, appears to competitively exclude the exotic, *H. mabouia*, from diurnal refuges along a developed coastline (Williams et al. 2016). Despite overlapping refuge preferences for the two species measured experimentally, surveys showed that *P. pulcher* had significantly higher densities in suitable diurnal refuges while *H. mabouia* was relegated to inferior diurnal refuge habitat (Williams et al. 2016). This indicates that *H. mabouia* was not able to displace *P. pulcher* from its preferred diurnal refuge (Fig. 4).

More frequently documented are the ways in which exotic geckos may negatively impact native gecko species. In Anguilla, *H. mabouia* may competitively exclude the native gecko, *Thecadactylus rapicauda*, based on the relative absence of *T. rapicauda* on buildings where *H. mabouia* was present (Howard et al. 2001; Fig. 4). *Thecadactylus rapicauda* is not exclusively edificarian, however, and the study does not discuss whether interactions occur in natural habitat. *Hemidactylus mabouia* is also thought to be displacing the

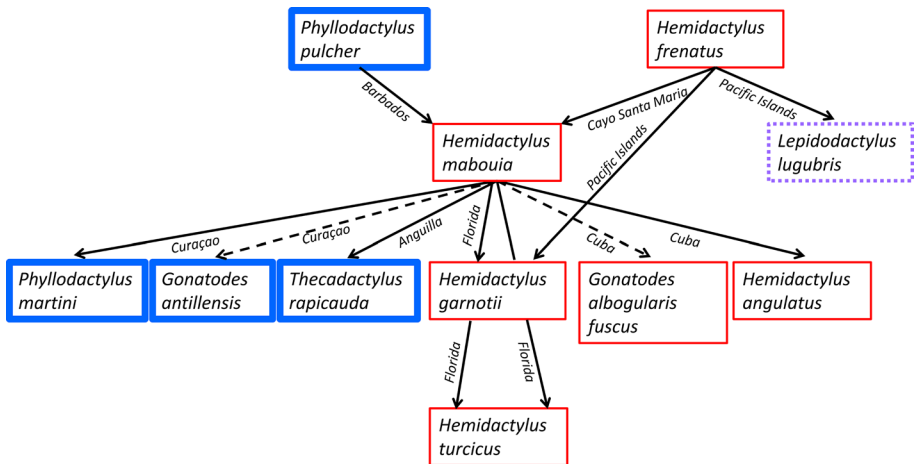


Fig. 4 Summary of interactions between gecko species; arrow points from interaction ‘winner’ to interaction ‘loser’. Arrow labels indicate locality where interaction has been documented. Solid arrows indicate an interaction is supported by experimental or observational data, whereas dashed arrows indicate interactions inferred from data. Thick boxes (blue) indicate native species in the Caribbean, thin boxes (red) indicate exotic species, and dotted box (purple) indicates the interaction was documented for *L. lugubris* both in its native (Pacific Basin) and exotic (Hawaii) range. See text for descriptions of studies that document the interaction. Color is visible in online version

native gecko, *Phyllodactylus martini* (and *Gonatodes antillensis*, but to a lesser extent), on Curaçao (Hughes et al. 2015; Fig. 4). Hughes et al. (2015) suggest two mechanisms of displacement. First, *P. martini* avoids brightly lit areas and is largely restricted to the forest, whereas *H. mabouia* is not restricted by proximity to the forest or avoidance of artificial light. In fact, *H. mabouia* and other edificarian geckos are often found using the “night-light niche,” in which they presumably benefit from greater abundance of prey and thermoregulatory advantages provided by artificial lighting (Perry et al. 2008). Second, saurophagy of *P. martini* by *H. mabouia* may be occurring. Though authors did not find evidence of saurophagy at the time, Dornburg et al. (2011) found *G. antillensis* remains in the stomach of one of 17 *H. mabouia* specimens collected from Curaçao, and in a later study, several authors observed predation of a juvenile *P. martini* by a large *H. mabouia* (Dornburg et al. 2016). Clearly there is a need for additional studies of competition between exotic and native gecko species in the greater Caribbean region, especially research that explores whether these interactions are occurring in natural habitats or only in anthropogenic settings.

While exotic geckos are likely to compete most strongly with other geckos, they are also generalist predators, preying a range of vertebrates and invertebrates that they encounter and are able to subdue. Therefore, as predators, they may interact with a wider range of native species and can have a stronger ecological impact as a predator than as a competitor (Kraus 2015), especially in island ecosystems (Doherty et al. 2016). The magnitude of the impact of exotic gecko predators on native species is determined, in part, by the habitat they use and their size. Edificarian gecko species like *H. mabouia* will have a disproportionately larger impact on disturbance-tolerant species than disturbance-sensitive species that avoid development. In comparison, larger species and species that spread from disturbed habitat into undisturbed, natural habitats could have sizeable ecological impacts (Meshaka et al. 1997; Breuil 2011). For example, one of the largest exotic geckos in the

greater Caribbean region, *Gekko gecko* (snout vent length ca. 150 mm), predated invertebrates and vertebrates, including other lizards, bats, rats, and snakes. It has been described as having a similar ecological impact in residential areas as cats, and may tolerate natural habitats (Meshaka et al. 1997; Aowphol et al. 2006; Breuil 2011; Bucol and Alcalá 2013). In Lee County, Florida, *G. gecko* was observed eating a native juvenile corn snake, *Elaphe guttata* (Love 2000). In another instance in Florida, *G. gecko* was observed to successfully consume *Romalea guttata*, a grasshopper species native to the southeastern United States, which is significant as only one species of bird is known to successfully feed on *R. guttata*, which releases a defensive chemical secretion when stressed and causes gagging, regurgitation, and even death in species that attempt to ingest it (Beauchamp and Mazzotti 2010). Although *G. gecko* currently has a limited exotic range in the greater Caribbean region (Behm et al. 2019), we predict that this species could have significant impacts as a predator as it spreads.

Interactions among established exotic gecko species in the greater Caribbean region

In locations with multiple established exotic gecko species, exotic geckos have had perceived or documented effects on each other. In Cuba, populations of the exotic gecko, *G. albobularis fuscus*, have declined during the time in which *H. mabouia* populations increased in the city of Havana (Fig. 4), though *G. albobularis fuscus* still remains common in some localities where only *H. angulatus* is present (Díaz 2014). Similarly, *H. angulatus* was abundant in Havana until the late 1990s, but in the 2000s *H. mabouia* became the most common species, partially displacing *H. angulatus* (Díaz 2014; Fig. 4). However, on Cayo Santa Maria, (Cuba bank) *H. frenatus* was nearly 12 times as abundant as *H. mabouia* which either reflects that *H. mabouia* was introduced more recently to Cayo Santa Maria than *H. frenatus*, or that *H. frenatus* is competitively dominant (Díaz 2014; Fig. 4).

In various locations in southern Florida and the Florida Keys, *H. turcicus* seems to have been largely displaced by *H. garnotii* and/or *H. mabouia* by the early 1990s (Meshaka et al. 1994b; Meshaka 1995), and by 2000, both *H. turcicus* and *H. garnotii* appeared to be outnumbered by *H. mabouia* (Meshaka 2000; Fig. 4). In Everglades National Park, between sampling periods in 1991–1992 and 1995–1996, *H. mabouia* colonized rapidly, spreading to new buildings and outnumbering *H. garnotii*, despite only marginal diet overlap between the two species, no significant difference in mean body size, and continuous egg-laying season shared by both species (Meshaka 2000). Mechanisms of displacement suggested by Meshaka (2000) include exploitative competition through territoriality of *H. mabouia*, saurophagy, and/or social dominance.

A similar study of interactions between *H. mabouia* and *H. garnotii* in southern Florida documented changes in species abundances consistent with a density-dependent mechanism of displacement. This insinuates that the decline of *H. garnotii* is linked to an increase in *H. mabouia* and that overall, *H. mabouia* appears to have a superior competitive ability as it reaches a higher carrying capacity than *H. garnotii* (Short and Petren 2012). The authors suggest exploitative competition, saurophagy, or social dominance as mechanisms for the decrease in abundance of *H. garnotii* and increase in *H. mabouia* in southern Florida (Short and Petren 2012).

Impacts of exotic geckos outside the greater Caribbean region

In general, the mechanisms underlying the interactions between the exotic gecko species found in the greater Caribbean region and resident geckos have been better documented in the exotic ranges of these species outside of the Caribbean. Knowing these mechanisms may allow predictions for the outcome of interactions between exotic and native gecko species within the Caribbean region. For example, two types of interactions could explain patterns of higher abundance of exotic *Hemidactylus frenatus* compared to native *Lepidodactylus lugubris* on islands in the tropical Pacific: predation of juvenile *L. lugubris* by *H. frenatus* (observed in lab) and territorial exclusion of *L. lugubris* by *H. frenatus* (observed in lab and field) (Case et al. 1994; Fig. 4). However, in Hawaii where both *H. frenatus* and *L. lugubris* are exotic, displacement of *L. lugubris* by *H. frenatus* is due to a different mechanism, namely that *H. frenatus* better exploits insect resources (Petren and Case 1996; Fig. 4). Experimental trials in Hawaii showed that an increase in *L. lugubris* density had a negligible effect on *H. frenatus*, but the foraging success of *L. lugubris* was significantly reduced in the presence of *H. frenatus*, leading to slightly negative impacts on *L. lugubris* mean body condition, fecundity, and survivorship (Petren and Case 1996). It is thought that human development facilitates these interactions due to the increased clumping of insect resources around artificial lights (Petren and Case 1996). Finally, *H. frenatus*'s sprint speed is four-times faster than *L. lugubris*, which may explain the competitive superiority of *H. frenatus* over *L. lugubris* (Niewiarowski et al. 2012).

In the Mascarene Islands in the Indian Ocean, *H. frenatus* competitively excludes native species *Nactus durrelli* and *N. coindemirensis* from refugia, leaving them more vulnerable to predation and other risks (Cole et al. 2005). Additionally, *H. frenatus* was observed in several cases to stalk and bite both native *Nactus* species, resulting in individuals of *N. coindemirensis* losing toes and tails and one case of predation (Cole et al. 2005). Although *Nactus* geckos are endemic to Oceania and do not occur in the greater Caribbean region, they are ecologically similar to *Sphaerodactylus* geckos endemic to the Caribbean that co-occur with exotic *H. frenatus* populations.

Experimental trials tested the hypothesis that resource competition or male aggression were the mechanisms for the global displacement of *H. garnotii* by *H. frenatus*. Resource consumption by *H. garnotii* was not impacted by *H. frenatus*, suggesting that resource competition is not the primary mechanism of displacement (Dame and Petren 2006; Fig. 4). Additionally, male aggression only occurred among *H. frenatus* males, not towards *H. frenatus* females or *H. garnotii*, which is an all-female parthenogenic species (Dame and Petren 2006). Thus, neither resource competition nor competitive interference through male aggression were found to be primary displacement mechanisms. The authors believe that sexual interference could be a likely mechanism of displacement because interspecific courtship was observed. However, it is not known whether interspecific mating actually disrupts parthenogenic reproduction in a way that would explain the observed levels of displacement (Dame and Petren 2006).

Introduction of novel parasites and pathogens to native species

The introduction of parasites and pathogens is a well-accepted threat posed by exotic species (Kraus 2015; Chalkowski et al. 2018), but it has received limited attention in Caribbean geckos (Martínez Rivera et al. 2003). Pentastomid endoparasites from the *Raillietiella*

genus and ectoparasitic mites from the *Geckobia* genus native to the paleotropics have likely been introduced to the Caribbean with their *Hemidactylus* hosts (Riley et al. 1991; Martínez Rivera et al. 2003). In particular, the mite, *Geckobia hemidactyli*, was found on wild-caught *H. mabouia* in Florida and Puerto Rico, as well as on preserved *H. mabouia* specimens collected from a range of Caribbean Islands (Martínez Rivera et al. 2003; Corn et al. 2011). *Geckobia* are likely transmitted via physical contact between individuals during sexual and territorial encounters or by using shared refugia (Bauer et al. 1990; Martínez Rivera et al. 2003). This may limit opportunities for exotic species to transmit *Geckobia* to native geckos, but it has not been extensively explored. On their own, ectoparasitic mites may cause reduced fitness, however, they may also transmit blood parasites (Allison and Desser 1981) and may serve as novel vectors for introduced and/or native blood parasites (Hoskin 2011). Exotic species can also be infected by native parasites and generalist parasites introduced by other exotics. In Australia, the pentastome parasite, *R. frenata*, was introduced with *H. frenatus* in 1976, but had a discontinuous and localized distribution that matched *H. frenatus*'s clustered distribution in urban areas (Kelehear et al. 2013). However, the introduction of the invasive cane toad (*Rhinella marina*) in 2006 provided *R. frenata* an alternative host with a more continuous distribution which facilitated the spread of *R. frenata* into new areas (Kelehear et al. 2013). At this point, more work is clearly needed to understand whether exotic geckos are introducing and/or facilitating the spread of parasites and/or pathogens in the greater Caribbean region.

Overall gecko interactions

We compiled the documented and predicted interactions from all studies with observational and/or experimental data supporting species interactions described above to make inferences about probable impacts of exotic geckos on other geckos in the greater Caribbean region (Fig. 4). At this point, *Hemidactylus mabouia* and *H. frenatus* appear to be the most dominant exotic species, but more studies are needed to explore the full range of impacts. Outside the Caribbean, *H. frenatus* negatively impacts a range of species using different mechanisms. Given the increasing spread of *H. frenatus* across Caribbean islands (Behm et al. 2019), it may cause significant displacement of native species. For the majority of Caribbean studies, the mechanisms of displacement are hypothesized but are not well-demonstrated. The uncertainty surrounding the mechanisms by which introduced gecko species negatively impact native ones is a gap in the invasion literature in the Caribbean that should be addressed, and future studies documenting how exotic geckos impact the surrounding ecosystem are badly needed.

Management and policy options

Given the extensive spread of exotic geckos and their associated negative ecological impacts, we compiled an overview of what management and policy options may be most effective for controlling their spread. Overall, preventing introductions of new exotic geckos should be a priority, especially due to the difficulty of detecting and eradicating established exotic populations (Mack et al. 2000; Myers et al. 2000; Keller et al. 2007). The monetary costs of controlling an exotic species post-introduction far outweigh the costs of prevention (Mack et al. 2000; Westphal et al. 2008; Kraus 2009). In addition, eradication options for exotic geckos are not well-developed and the likelihood of successful eradication is low (Pitt et al. 2005). However, if a species causes substantial negative impacts, a

variety of targeted control and/or eradication methods are likely to be developed, such as those used in efforts to eradicate the brown treesnake (*Boiga irregularis*) in Guam (Perry et al. 1998; Johnston et al. 2002). Therefore, stronger regulations including the development of risk assessments for species and screening measures for unintentional movement in cargo, as well as more stringent pet-trade regulations, are recommended.

Many studies have attempted to model and predict what characteristics of species or geographic regions are susceptible to invasion. Habitat and climate matching, propagule pressure, and invasion history are generally helpful in predicting successful invasions across taxa (Hayes and Barry 2008; van Wilgen et al. 2009; Rago et al. 2012). By documenting the pathways by which geckos have been introduced to the greater Caribbean region, when known, we have attempted to further the understanding of how species are moved so that it can be incorporated into management planning and creation of risk assessments.

For species commonly introduced via passive cargo, like many *Sphaerodactylus* species, screening and quarantine of imports that are at high-risk for containing hitchhikers, such as lumber or agricultural products, is the best way to prevent this kind of introduction (Kraus 2009). Understanding which shipping routes, packing material, or type of cargo has led to introductions in the past may allow for greater screening success (Kraus 2009). It is also suggested by Kraus (2009) that for the Caribbean islands, because many of the countries are too small or do not have enough data to create country-specific risk assessments, a regional analysis is useful to determine cargo-inspection priorities. Indeed, since the nursery trade from southern Florida is the primary contributor of exotic reptiles and amphibians to the Caribbean (Powell et al. 2011; Krysko et al. 2016), resources should be devoted to inspecting these shipments. In addition to port inspections, policy tools including trade tariffs and tradable risk permits may also be useful in preventing accidental introductions of exotic species as well as combating the externalities associated with a species becoming invasive (McAusland and Costello 2004; Horan and Lupi 2005; Westphal et al. 2008).

Stricter regulations on the intentional import of geckos and other herpetofauna for commercial use, such as the pet trade, is also necessary in the Caribbean islands and their major trade partners like the United States. Regulations currently in place to prevent negative impacts on endangered species through trade, such as the US Endangered Species Act (ESA) and Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), are limited in the diversity of species they protect and the means by which they protect them, and reflect the reactionary rather than preventative nature of most government initiatives (Smith et al. 2009b). For herpetofauna, the majority of the most commonly traded species are not regulated by ESA or CITES (Schlaepfer et al. 2005). Furthermore, these laws are meant to prevent negative impacts on endangered species through regulating their international trade without considering the potential impacts caused by exotic introductions of species and/or pathogens (Smith et al. 2009b). The US Fish and Wildlife Service (USFWS) keeps records of all legally imported and exported wildlife through their Law Enforcement Management Information Systems (LEMIS) database (Schlaepfer et al. 2005). However, these records often do not report imports and exports to species-level, sometimes only recording them in a general “non-CITES” category (Schlaepfer et al. 2005; Smith et al. 2009b). For example, between 1998 and 2002, over 1 million wild-caught geckos were imported into the United States without species-level identifications recorded in the LEMIS database (Schlaepfer et al. 2005). In the bird trade, birds that are wild-caught rather than captive-bred have been among the most successful invaders even if they are not among the most common in the pet trade (Carrete and Tella 2008), which is another facet to explore regarding trade of wild-caught geckos. Adoption of more stringent protocols for species-level record-keeping in the LEMIS database can allow more

rigorous and comprehensive risk analysis of the full diversity of species being imported into the United States and those being exported to the Caribbean and other regions (Smith et al. 2009b). The Caribbean region and other countries or regions may consider looking to countries with tighter trade regulations, such as Australia and New Zealand, as a model for implementing such measures (Smith et al. 2009b; García-Díaz and Cassey 2014).

While government regulations are an important way to combat exotic introductions through the pet trade, even blanket wildlife trade bans, such as those in place in Australia, are not completely effective (García-Díaz and Cassey 2014). The private pet trade industry as well as pet owners and hobbyists must also be held responsible. It has even been recommended that funds be collected directly from the pet trade and applied to programs such as training for local response teams to capture released pets, incentive programs for pet stores and breeders to take back unwanted pets, and a system by which pet owners can be identified and punished for releasing their animals (Perry and Farmer 2011). It may also be useful to implement public education programs regarding exotic pets to supplement policy action for lasting results. A combination of direct action and communication with the public was the most effective at reducing the abundance of *Trachemys scripta elegans*, a turtle common in the pet trade, in freshwater ecosystems in France (Teillac-Deschamps et al. 2009). Education programs should both encourage a positive perception toward nature and biodiversity conservation as well as focus on the issues surrounding the release of exotic pets into natural habitat and the risks of invasive species (Masin et al. 2014).

Conclusions

Understanding the drivers and pathways of exotic species spread is a pivotal step in curtailing their distribution and impacts. We predicted that most exotic geckos in the greater Caribbean region would be spread unintentionally as stowaways in cargo as has been suggested by Kraus (2009) and documented in New Zealand (Chapple et al. 2016). While unintentional spread was a substantial pathway in the Caribbean islands, many species were also spread intentionally via the pet trade, predominantly in Florida. As such, patterns exhibited by geckos may also share similarities with species spread intentionally, like birds and plants, in the Caribbean and elsewhere (e.g., Reichard and White 2001; Cassey et al. 2004; Russello et al. 2008). Furthermore, our findings may indicate that other species that are thought to be spread by one particular pathway may actually be spread by multiple pathways, which requires a multifaceted and/or prioritization management approach (McGeoch et al. 2016).

We also predicted that the greater Caribbean region would have more exotics due to high import rates within islands, and high rates of species endemism. While it does appear that islands with higher economic activity have more exotic species, over two-thirds of the exotic geckos in our dataset are endemic to regions *outside* the Caribbean, indicating that local endemism is not the only factor contributing to the number of exotic species in the greater Caribbean region. Notably the exotic geckos endemic to regions outside the Caribbean were predominantly introduced via the pet trade to Florida. This indicates that the high within-Caribbean endemism currently may be a contributing factor to exotic spread among the Caribbean islands but could shift if the pet trade becomes more prominent on Caribbean islands. Although an in-depth statistical analysis of which factors contribute to the numbers of exotic species in the greater Caribbean region versus other regions is beyond the scope of our study, economic activity as well

as the sensitivity of islands to being colonized by exotic species may be important (Simberloff 1995; Lonsdale 1999; Westphal et al. 2008; Sax and Gaines 2008; Hulme 2009). Future work examining these variables in a comparative context among regions would be fruitful.

Our review shows that exotic gecko species are clearly spreading across the greater Caribbean region and at an accelerating rate. The lack of details surrounding most introductions suggest that gecko species likely go undetected for some time after introduction, which may provide the opportunity for establishment and spread, and reduce the potential for successful eradication (Myers et al. 2000). We suspect that many exotic geckos are documented only after establishment, which may explain the high establishment success we found relative to other exotic herpetofaunal species in other locations (Kraus 2009; Krysko et al. 2016). Accordingly, unsuccessful introductions that fail to establish likely evade detection and go unreported, indicating that our review under-estimates the total number of introductions, which is common for many taxa, not just geckos (McGeoch et al. 2010). In addition, more exotics may be present than reported because species such as *Lepidodactylus lugubris* and species in the *Hemidactylus* genus resemble each other from a distance, such that new invaders may be misidentified as a resident exotic without close inspection (Alonso Bosch and Borroto Páez 2017; Behm et al. 2019).

Given the strong relationship between establishment success and propagule pressure demonstrated in other systems (Cassey et al. 2004; Lockwood et al. 2005; Blackburn et al. 2013), the high establishment success of exotic geckos in the greater Caribbean region may also indicate high propagule pressure. This high propagule pressure could be due to a single introduction of a large number of individuals, or multiple separate introductions of individuals which has been demonstrated for many species, including *Anolis* lizards in the Caribbean (Kolbe et al. 2007). Using genetic methods to identify introduction patterns such as multiple introductions for exotic geckos would further inform management efforts.

Looking forward, we suggest focusing conservation efforts along two main avenues. First, we strongly recommend research attention be focused on understanding the impact of exotic geckos on native species and ecosystems. Political support and funding for responding to invasive herpetofauna is unlikely without greater evidence of negative impacts (Kraus 2009). Although not currently available, new IUCN evaluations of Caribbean reptiles are forthcoming (S.B. Hedges, *pers. comm.*), which are predicted to show high levels of endangerment (Wilson et al. 2011). Thus, understanding the impacts of exotic species on sensitive native geckos is a conservation imperative. Furthermore, given that even less is known about terrestrial Caribbean invertebrates, the effects of exotic geckos as generalist predators could potentially cause substantial negative impacts on uncatalogued biodiversity.

Second, considering the low predicted success of eradication efforts, we strongly advocate measures to prevent new introductions of exotic geckos. This includes measures at locations without exotic geckos to prevent new introductions, and measures at locations with exotic geckos and geckos with the potential to be exotic to prevent their spread to new locations. Although there is no indication that the current trajectory of exotic gecko introductions will slow in the near future, it is still early in the invasion process regionally as many islands still have only one exotic gecko species. By enacting a combination of the measures recommended above, the introduction, establishment, and spread of exotic geckos and other species can be reduced.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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