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EXOTICS EXHIBIT MORE
EVOLUTIONARY HISTORY
THAN NATIVES:
A COMPARISON OF THE
ECOLOGY AND EVOLUTION
OF EXOTIC AND NATIVE
ANOLE LIZARDS

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Abstract

Long-distance colonization was once rare causing species within regions to be closely related. Now, in the Anthropocene, biogeographic structure is being eroded by species introductions. Here, we contrast the ecology and evolution of native versus exotic Caribbean *Anolis* lizards and show that the once strong biogeographic structure in the clade has been altered by the introduction of 22 *Anolis* species. Anole introductions are more frequent and span greater distances than natural anole colonizations. As a result, exotic anole populations in the Anthropocene often contain more genetic diversity than native populations, and anole phylogenetic diversity on islands is rapidly increasing.

INTRODUCTION

In the past, the rate at which species colonized new areas, such as distant islands, was relatively slow, and long-distance dispersal events were rare. As a result, species within biogeographic regions shared much of their evolutionary history; for any given species group, closely related species tended to be found in the same region. Within species, populations were further subdivided due to limited dispersal, assortative mating, and vicariance events resulting in phylogeographic patterning of populations. Today, this strong spatial patterning of evolutionary history is eroding. In an epoch in which earth systems are dominated by humans—the Anthropocene—species are frequently and often unintentionally transported far from their native regions. These long-distance dispersal events due to humans (i.e., species invasions) are occurring at rates much higher than in the past, causing the evolutionary history that underlies the geography of many organisms to become irreversibly mixed. Here, we describe this mixing of evolutionary history for a well-studied radiation of species from the lizard genus *Anolis* (or anoles). These lizards have naturally colonized Caribbean islands for millennia, and in the Anthropocene continue to be one of the most prolific groups of colonizing species.

Endemic to the Americas, over the past tens of millions of years the *Anolis* lizard radiation has produced approximately 165 Caribbean and 210 mainland species. Anoles are adapted to a multitude of tropical and

subtropical habitats and exhibit a wide diversity of ecological morphologies and geographic range sizes. They are a model clade for understanding the ecological and evolutionary processes that give rise to biogeographic and phylogeographic patterns, especially across islands (Losos 2009). Before European settlement of the Americas, anoles infrequently colonized new land masses. Those colonizations that did occur were usually only from proximate areas (Williams 1969). There have been approximately 40 colonizations of Caribbean island banks over the past 60 million years as estimated by phylogenetics (Helmus & Ives 2012; Losos 2009; Mahler *et al.* 2010; Nicholson *et al.* 2005). Yet since European settlement of the Caribbean, there have been approximately 40 exotic colonizations, with the rate increasing over time. Before World War II (WWII), there were 0.07 (± 0.01 SE) new exotic anole colonizations per year in the Caribbean. As of 2015, the rate is 0.96 per year (± 0.12), a 14-fold increase since the end of WWII (Helmus *et al.* 2014). While making a robust comparison between past and Anthropocene colonization rates is difficult as the sources of the underlying data are different—phylogenetics versus field surveys—the message is clear: anoles are in an unprecedented age of range expansion.

Anoles have been introduced by humans across the globe and are now found far from the Americas (Fig. 1). The introduction of exotic anoles has been intentional at times, yet the majority of introductions to Caribbean islands have likely been unintentional via the shipment of live plants for landscaping and agriculture (Helmus

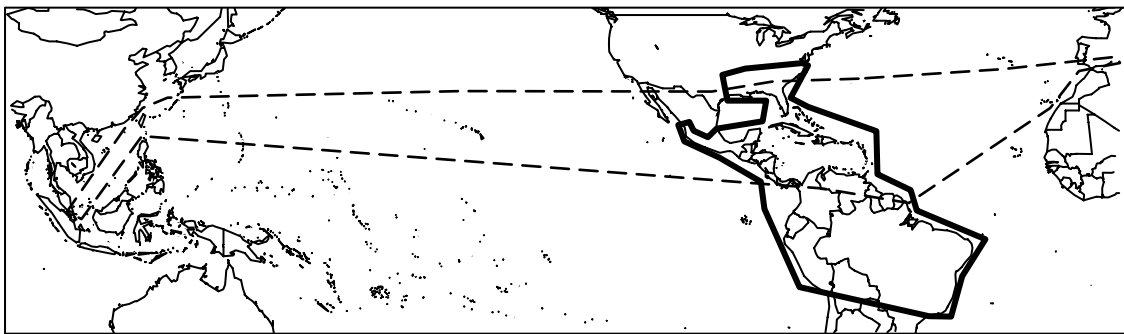


Fig. 1 The global range limits of native and exotic *Anolis* lizards. The thick solid line delineates the distribution of native *Anolis* and the dashed line roughly delineates exotic anole distribution limits as of 2015. Nations/territories with an established exotic anole are Anguilla, Aruba, Bahamas, Barbados, Belize, Bermuda, Canary Islands, Cayman Islands, Costa Rica, Curaçao, Dominica, Dominican Republic, French Guyana, Grenada, Guam, Guyana, Jamaica, Japan (Okinawa, Ogasawara Islands), Mexico, Northern Mariana Islands, Puerto Rico, St. Lucia, St. Maarten, St. Vincent and the Grenadines, St. Thomas, Singapore, Spain, Suriname, Taiwan, Trinidad and Tobago, the United States (mainland, Hawaii), and Venezuela.

et al. 2014; Kraus 2009; Losos *et al.* 1993; Perry *et al.* 2006; Powell *et al.* 2011). Before humans, anoles that established on Caribbean islands spread within intact ecosystems that typically contained few resident anole species. In contrast, exotic anoles in the Anthropocene establish into heavily disturbed natural and newly emergent anthropogenic habitats (e.g., resort gardens), encountering not only native species but also well-established exotics (Powell *et al.* 2011). The evolutionary and ecological processes that determine anole species diversity have thus greatly changed in the Anthropocene.

Here, we present a review focused on Caribbean anole species, as most exotic anoles are native to and have established in the Caribbean, not in the mainland. We have structured the review to contrast what is known regarding the natural dispersal and colonization processes of native anoles to the human-mediated translocation of exotic anoles in the Anthropocene. Our review follows the introduction process starting with transportation to a new location and ending with the stage where species adjust to local conditions. We highlight patterns of genetic variation and trait adaptation that have contributed to and are resultant of the success of native anole species and exotic populations. Because predicting the spread of exotic species is a major challenge in the Anthropocene, we follow with a description of the macroecological patterns in exotic distributions and how the evolutionary history resulting from exotic introductions differs from the natural biogeographic patterns exhibited by natives. Finally, we conclude the review with insight into the future evolution of anoles in the Anthropocene.

TRAVEL TO NEW CARIBBEAN ISLANDS

Any terrestrial species, regardless of whether they are dispersing naturally or assisted by humans, must first successfully travel over water in order to colonize a new island. For the vast majority of their evolutionary history, in the absence of human assistance, the main overwater dispersal vector for anoles was vegetative flotsam (Hedges 2001). Successful transit was dependent on prevailing currents and winds, whereby individuals had to survive desiccation, solar radiation, and starvation while clinging to vegetation that had been blown out to sea. In the Anthropocene, the majority of exotic anoles also arrive to new locations via plants that are transported by humans for agriculture and the live plant trade (e.g., Perry *et al.* 2006). One of the

earliest documented exotic colonizations in the Caribbean via live plants occurred in the early 1800s (recounted in Lazell 1972). In 1789, the British HMS *Bounty* captained by William Bligh of the Royal Navy was returning from Tahiti with a shipment of breadfruit saplings to be planted on St. Vincent island in the Caribbean. The ship never completed the journey as its crew mutinied, placing Bligh and loyal crew members on a small launch in middle of the South Pacific (i.e., *The Mutiny on the Bounty*). Bligh improbably survived and a couple years later succeeded in the voyage, establishing breadfruit on St. Vincent. A decade later, breadfruit cultivars from Bligh's St. Vincent plantation were transported to Trinidad. This live plant shipment from St. Vincent to Trinidad contained not only the fruit trees but also the St. Vincent bush anole (*Anolis trinitatis*) that is native only to St. Vincent. *Anolis trinitatis* established and became a naturalized part of the Trinidadian herpetofauna so much so that it was first described as a species endemic to Trinidad, hence the misnomer *trinitatis*.

Anolis trinitatis is one of 22 anole species that have established exotic populations in the Anthropocene (Table 1). The majority of exotic anole introductions in the Caribbean have been inadvertent via the live plant trade, although many, especially in Florida, were due to the pet trade (Krysko *et al.* 2011). Of the 38 exotic colonizations on Caribbean islands, 22 have known introduction vectors: 18 (82%) were transported by cargo shipments, primarily live plants, and 4 were intentionally released for various reasons (Table 2; see extended data table 1 in Helmus *et al.* 2014). There have also been several experimental introductions of anoles, primarily *Anolis sagrei*, to small satellite islands such as in the Bahamas, where it is native, and islands in Florida, where it is exotic, to test biodiversity theory (e.g., Kolbe *et al.* 2012a; Stuart *et al.* 2014). However, these experimental introductions relocate anoles very short distances to islands within their native or well-established exotic ranges compared to most unintentional introductions that result in the establishment of exotic anoles far from their native ranges.

Because surviving long time periods clinging to flotsam is difficult and Caribbean island banks are separated by deep water and long distances, successful among-bank natural dispersal events are relatively rare, and occurred in the past most often among proximal land masses. As a result, stepping-stone patterns of colonization and allopatric speciation are evident in the anole phylogeny (Thorpe *et al.* 2004). For

Table 1 List of *Anolis* lizard species that have had exotic populations as of 2015

Exotic <i>Anolis</i>	Ecological morphology	Number of colonizations	Native to	Genetics reference
<i>sagrei</i>	Trunk-ground	>10	GA	Kolbe <i>et al.</i> (2004)
<i>crisatellus</i>	Trunk-ground	≥5	GA	Eales <i>et al.</i> (2008)
<i>cybotes</i>	Trunk-ground	≤3	GA	Kolbe <i>et al.</i> (2007)
<i>carolinensis</i>	Trunk-crown	≥5	GA*	Sugawara <i>et al.</i> (2015)
<i>chlorocyanus</i>	Trunk-crown	≤3	GA	Kolbe <i>et al.</i> (2007)
<i>grahami</i>	Trunk-crown	≤3	GA	Chakravarti (1977)
<i>maynardi</i>	Trunk-crown	≤3	GA*	
<i>porcatus</i>	Trunk-crown	≤3	GA	Kolbe <i>et al.</i> (2007)
<i>smaragdinus</i>	Trunk-crown	≤3	GA*	
<i>distichus</i>	Trunk	≤3	GA	Kolbe <i>et al.</i> (2007)
<i>equestris</i>	Crown-giant	≥5	GA	Kolbe <i>et al.</i> (2007)
<i>garmani</i>	Crown-giant	≤3	GA	Kolbe <i>et al.</i> (2007)
<i>aeneus</i>	Small LA	≤3	LA	
<i>pogus</i>	Small LA	≤3	LA	
<i>trinitatis</i>	Small LA	≤3	LA	
<i>wattsi</i>	Small LA	≤3	LA	
<i>extremus</i>	Intermediate LA	≤3	LA	
<i>marmoratus</i>	Intermediate LA	≤3	LA	
<i>bimaculatus</i>	Large LA	≤3	LA	
<i>leachii</i>	Large LA	≤3	LA	
<i>richardii</i>	Large LA	≤3	LA	
<i>lineatus</i>	Unknown	≤3	SA	

The number of *colonizations* gives an estimate of the number of times each species has established a reproducing exotic population. Note that exotic *Anolis pogus* and *Anolis bimaculatus* populations are considered extirpated. *Trunk*, *trunk-ground*, *trunk-crown*, and *crown-giant* are ecomorphs that evolved across the Greater Antilles. *Small*, *intermediate*, and *large LA* are body sizes that evolved across the Lesser Antilles. See Losos (2009) for a review of these morphologies.

* Indicates species recently derived from a natural colonization from Cuba (i.e., the *carolinensis* clade). *Genetics reference* gives an example reference, if one exists, of an invasion genetics study on the species.

example, an ancestor from the Puerto Rican bank likely colonized the islands of the northern Lesser Antilles in a roughly stepping stone fashion from north to south, where each colonization led to an allopatric speciation event and formed part of the large-bodied *bimaculatus* clade (Stenson *et al.* 2004). Phylogenetic analyses also indicate that the anoles native to the southern Lesser Antilles were likely derived from a single colonization of an ancestor population from northern South America, which then allopatrically speciated northward up the island chain in a roughly stepping-stone fashion to Martinique (Creer *et al.* 2001; Thorpe *et al.* 2004). In comparison, exotic anole colonizations are not limited by geographic isolation. Rather, economic connectivity dictates translocation such that islands with ports that receive large amounts of shipping traffic have the most exotic anoles (Helmus *et al.* 2014).

The mainland (i.e., Mexico, Central America and South America; Fig. 1) has a higher number of native anole species compared to the Caribbean Islands (~210 vs. 165 species), yet all anole species with exotic populations are native to Caribbean islands except one, *Anolis carolinensis*. This disparity in invasion success between Caribbean and mainland anole species is likely due to two main factors. First, Caribbean anoles are more likely than mainland anoles to have native ranges that encompass shipping ports and thus are more likely to be inadvertently transported out of their native range (Latella *et al.* 2011). As an exception that proves the rule, *A. carolinensis* has a native range that encompasses several major shipping ports in the Southeastern United States (e.g., Miami and New Orleans), and it has spread to the Lesser Antilles and as far as Hawaii and Okinawa.

Table 2 Characteristics typifying native and exotic *Anolis* lizard species

	Natives	Exotics (as of 2015)
Number of species	375 total (possibly >400) 165 Caribbean species	22 species have had exotic populations 36 extant (2 extirpated) populations across Caribbean islands
	209 in Mexico, Central America, South America 1 in the United States	55 extant populations worldwide (rough estimate) 10 in the United States (most of any country)
Transport vector	Vegetative flotsam	Unintentional transport—frequently via the live plant trade Intentional transport—pet trade, biocontrol, experiments
Traits needed to survive journey	Tolerance to desiccation, starvation, and thermal extremes	Tolerance to desiccation, starvation, and thermal extremes; may differ depending on vector
Spatial extent of colonization	Proximal to source range	Can be far from native source range (e.g., Spain and Taiwan)
Temporal rate of establishment	40 in 40–60 million years (rough estimate)	1 per year in the Caribbean
Genetic diversity of populations	High genetic variation among populations despite small geographic ranges Low variation within populations	Reduced variation through founder effects in some populations High variation within populations due to multiple introductions and subsequent admixture
Adaptation to local conditions	Repeated adaptation to abiotic/biotic environmental variation resulted in widespread convergent evolution of similar ecomorphs	Rapid adaptation in multiple traits: scale density, limb size, toepad size, body size, head shape, thermal tolerance, perching behavior, foraging behavior, territorial displays
Phylogenetic diversity of island assemblages	Generally low due to infrequent natural colonizations from proximate regions and subsequent speciation resulting in closely related species	Generally high due to frequent long-distance colonizations of distantly related species

The second major factor that makes Caribbean anole species more likely than mainland species to be exotic is that many Caribbean anoles have naturally evolved traits conducive to overwater colonization (Latella *et al.* 2011; Poe *et al.* 2011). For example, *A. sagrei*, the most prolific exotic anole (Table 1), has traits that confer desiccation, heat, and starvation tolerance essential for surviving the beach and dry forest scrub habitats where it is naturally found. These same traits are also essential to surviving long-distance ship travel. *Anolis sagrei* is also a natural overwater disperser. Individuals can survive for days to weeks without food, can float without rafts in seawater for long periods, and will actively swim away from inhospitable islets (Schoener & Schoener 1983a, 1984). Across species, Latella *et al.* (2011) performed a comparative analysis that included both Caribbean and mainland anoles and found that

species with exotic populations tended to be larger bodied, have larger scales, and be more sexually dimorphic in body size. Larger bodied anoles can survive longer without food and are competitively superior to smaller anoles (e.g., Pacala & Roughgarden 1985); larger scales may reduce inter-scale water loss and protect against solar radiation (Losos 2009; Wegener *et al.* 2014), while sexual dimorphism allows partitioning of resources between the sexes facilitating establishment in new environments (Schoener 1969a). Furthermore, those anole species that were good natural colonizers in the ancient past—as measured by native species distributions and an evolutionary reconstruction of anole biogeography—are the same species, or are closely related to species, that currently have exotic populations (Poe *et al.* 2011). Evolutionary history can therefore predict which anole species might become

exotic; however, the overall explanatory power of phylogeny in predicting exotic success is statistically weak as there has been much convergent evolution in anole traits that erases phylogenetic signal (Latella *et al.* 2011; Mahler *et al.* 2013).

Native and exotic transport to new islands is thus very similar (Table 2). The environmental stress of transport is similar, and as a result, the traits that make a good natural colonizer are the same as those that make a good exotic colonizer. The main dispersal vectors of both natives and exotics are also the same: plants. The differences are that in the Anthropocene, the vegetation (i.e., plant cargo) in which anoles are transported arrives to new islands at a much higher rate and from longer distances than plant flotsam. These differences in distance and rate have caused anoles that were once geographically relegated to the Americas for millions of years, to have dispersed across oceans to Asia and Europe within the past century (Fig. 1).

POPULATION GENETIC STRUCTURE

Native anole species often exhibit significant phylogeographic genetic structure whereby genetic variation among populations often exceeds within population variation. For example, *Anolis cooki* has a small geographic range restricted to the southwestern coast of Puerto Rico with the most distant populations being only 50 km apart, yet it exhibits strong phylogeographic structure caused in part by a river limiting gene flow between western and eastern populations. Rodríguez-Robles *et al.* (2008) found 27 unique mitochondrial haplotypes across *A. cooki*'s range with no populations sharing any haplotypes. Similarly, other species in Puerto Rico—*Anolis poncensis* with a small range like *A. cooki*, and *Anolis cristatellus* and *Anolis krugi* with wider distributions—exhibit significant population genetic differentiation and phylogeographic structure (Jezkova *et al.* 2009; Kolbe *et al.* 2007; Rodríguez-Robles *et al.* 2010). Anole species from the Lesser Antilles also exhibit high among-population genetic diversity (Thorpe *et al.* 2015). The endemic anole *Anolis oculatus* is widespread on Dominica and has high among-population genetic variation, such that most haplotypes are restricted only to single localities, and strong phylogeographic structure likely due to past vicariance events caused by volcanism (Malhotra & Thorpe 2000). The native anole species of Martinique (*Anolis roquet*) also exhibits high genetic variation

across the island with genetically subdivided populations that correspond to precursor species that diverged allopatrically on four separate ancient islands that later coalesced into the present-day Martinique (Thorpe *et al.* 2010). Therefore, anole species exhibit strong phylogeographic structure in their native ranges, and genetic variation among populations is naturally higher than within populations.

This strong phylogeographic structure in native anoles has made it possible to trace the source populations of exotic anoles. For example, *A. sagrei* was introduced to the Florida Keys in the latter half of the nineteenth century, and by the 1970s it had naturalized and spread throughout Florida. Genetic analyses indicated that exotic *A. sagrei* populations in Florida are the result of at least eight introductions from different source populations across its native range in Cuba (Kolbe *et al.* 2004). The independent introductions subsequently admixed in Florida, greatly increasing genetic variation within exotic populations (Fig. 2). This mode of invasion—multiple colonizations from

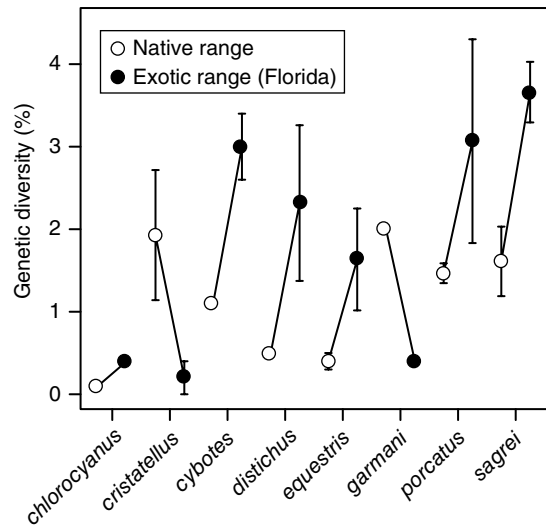


Fig. 2 The genetic diversity within exotic *Anolis* lizard populations in Florida is generally higher than the genetic diversity within populations in their native ranges. Genetic diversity is the mean pair-wise mtDNA sequence divergence of sampled individuals within populations. Points are means across populations, and standard errors are given for those means where multiple populations were sampled. Data are aggregated from Kolbe *et al.* (2004, 2007), which provide full descriptions of the data and statistical analyses.

geographically and genetically distinct source populations followed by admixture in the exotic range—has also occurred in four other exotic anole species in Florida: *A. cristatellus*, *Anolis cybotes*, *Anolis distichus*, and *Anolis equestris* (Fig. 2; Kolbe *et al.* 2007; Kolbe unpublished data). All of these species were derived from at least two introductions with *A. sagrei* derived from at least eight and *A. distichus* derived from at least four independent introductions. Similarly, the exotics *A. cristatellus* in the Dominican Republic and *A. sagrei* in Jamaica were also likely derived from at least two introductions from different parts of their native ranges (Kolbe *et al.* 2007).

The observations of high genetic variation in exotic populations and the ability of exotic populations to establish and spread are in contrast to the classically held view in invasion genetics that exotic populations should exhibit founder effects. Genetic founder effects occur when founding propagules possess a subset of the genetic variation exhibited in the ancestral population and are an expected consequence of oversea dispersal of only a few surviving individuals. Founder effects could result in reduced adaptive potential and inbreeding depression that limit population growth and ultimately the establishment success of a newly arrived species (Allendorf & Lundquist 2003). Experimental introductions of anoles to small islands have artificially induced genetic founder effects without adversely affecting population success. Schoener and Schoener (1983b) and Losos and Spiller (1999) introduced anoles to small islands in the Bahamas that were previously uninhabited by anoles. Despite the small numbers of founders (5–10 founding individuals per island), most of the populations persisted and almost all increased in population size for years and many continue to this day. In another experimental introduction, Kolbe *et al.* (2012a) founded seven small islands in the Bahamas with male–female pairs of *A. sagrei* that were randomly selected from a large island. The experiment produced strong genetic founder effects, yet all *A. sagrei* populations persisted and adapted to the new island environments (Kolbe *et al.* 2012a).

The species that naturally colonize islands may be adapted to resist the negative consequences of genetic founder effects, predisposing them to become successful exotic species (Baker 1955). For example, *A. carolinensis*, a good natural colonizer (Glor *et al.* 2005), was introduced to the Japanese island Chichi-jima in the 1960s and then spread to the nearby islands of

Ani-jima and Haha-jima. Even though the Ani-jima and Haha-jima populations have genetic founder effects (i.e., reduced genetic variation), the species has established and spread across both islands (Sugawara *et al.* 2015). Similarly, *A. cristatellus*, introduced to Dominica exhibits a genetic founder effect, yet in the decade that it has colonized Dominica, it has displaced the native anole *A. oculatus* from much of southwest Dominica where it is found (Eales *et al.* 2008). *Anolis cristatellus* in Florida also exhibits a possible founder effect (Fig. 2), yet since its establishment 40 years ago, it has spread and is abundant in some areas (Krysko *et al.* 2011). *Anolis garmani* was also introduced to Florida and exhibits a founder effect (Fig. 2). While it is localized and has not yet spread widely, it has been well-established since the 1970s (Krysko *et al.* 2011). Finally, *Anolis grahmi* introduced to Bermuda in 1905 exhibits a genetic founder effect (Chakravarti 1977), but it has naturalized and spread island wide. Although these preceding examples are of all successful establishments despite founder effects, it is not known if founder effects are the cause for failed anole introductions as these are rarely documented.

Successful exotic invasions in the context of single introductions with genetic founder effects may lend insight into the natural colonization process that occurred most certainly with low numbers of founding individuals. At present, the influence of founder effects on the establishment of native anole populations has not been well explored. In addition, invasion genetics in anoles needs further investigation—less than half of all exotic anoles species have had their population genetics sampled (Table 1)—but the most remarkable contrast emerging between native and exotic anoles is in their population genetic diversity (Table 2). Natives generally exhibit low within-population genetic variation, whereas exotic anoles can have very high within-population variation (Fig. 2).

RESPONDING TO ENVIRONMENTAL VARIATION

Across the Caribbean, native anole species exhibit morphological and behavioral adaptations to environmental selective pressures. Most notably, there is considerable variation in precipitation and vegetation structure within and across Caribbean islands. In the Lesser Antilles, some islands have distinct xeric coastal woodlands and wetter montane rainforests in the

interior. Conspecific populations collected from xeric and rainforest sites within the same Lesser Antilles island can show divergent adaptation to this climate variation in several quantitative traits such as body shape, scalation, and hue, which are correlated with survival in their respective environmental conditions (Ogden & Thorpe 2002; Thorpe *et al.* 2015). For example, the Dominican anole *A. oculatus* exhibits morphological variation that matches elevational habitat variation despite significant gene flow between populations along the gradient (Stenson *et al.* 2000, 2002). Similarly, *Anolis marmoratus* of Guadeloupe exhibits high variation in male dewlap color and skin pattern that corresponds to a gradient of mesic and xeric habitats within the context of high levels of interpopulation gene flow (Muñoz *et al.* 2013). Because gene flow in both *A. oculatus* and *A. marmoratus* has been quantified using neutral genetic markers, the correlation between trait variation and environmental variation may indicate divergence in the functional portions of the genome related to adaptive traits. This divergence of functional genes may be maintained by assortative mating among individuals with the same ecological phenotype. In Martinique, for example, assortative mating in *A. roquet* occurs between individuals with the same ecological phenotype along the elevation gradient, rather than between individuals with shared phylogeographic ancestry as indicated by genetic markers (Thorpe *et al.* 2010).

Experimental work suggests that adaptation to environmental conditions can be rapid, which may facilitate the colonization success of introduced populations. Losos *et al.* (1997) found that *A. sagrei* populations experimentally introduced to small islands of the Bahamas had, over the course of a little more than a decade, adapted morphologically to match the vegetation structure of the islands. Later, in a similar experimental introduction, Kolbe *et al.* (2012a) found the same result: *A. sagrei* hindlimb length decreased in response to narrower vegetation on the introduced islands; however, this morphological change occurred in just 4 years. Although *A. sagrei* exhibits phenotypic plasticity in limb length in response to perch diameter (Losos *et al.* 2000), the magnitude of divergence in limb diameter due to plasticity induced in laboratory experiments is less than the divergence observed in these experimentally introduced populations. This suggests that plasticity alone is insufficient to explain the changes in limb length over time, and that adaptation likely occurred (Kolbe *et al.* 2012a).

Rapid adaptation in response to the environment has also been observed in unintentionally introduced exotic anole populations. For example, in 10 years on Dominica, exotic populations of *A. cristatellus* at high elevation sites have evolved a lower scale density possibly in response to the wet, high-elevation environments compared to the dry, low-elevation environments where it was introduced (Eales *et al.* 2010; Malhotra *et al.* 2011). However, this scalation-elevation pattern seen for *A. cristatellus* on Dominica is opposite to the average pattern observed among anole species: species naturally found in drier climates have larger and lower densities of scales than species found in wetter environments (Wegener *et al.* 2014). The difference between the causes of scale variation among and within species needs further exploration (Losos 2009).

Exotic anoles have also adapted their thermal niches. Kolbe *et al.* (2014) found that *A. sagrei* populations from southern Georgia can tolerate significantly lower temperatures than Florida populations, suggesting that *A. sagrei* is evolving to withstand colder temperatures in its expanding northern exotic range. Similarly, *A. cristatellus* was introduced to Miami in the mid-1970s and since that time has become more thermally plastic by acquiring the ability to acclimate to lower temperatures than in its native range in Puerto Rico (Kolbe *et al.* 2012b; Leal & Gunderson 2012). This adaptability of exotics stems from the evolutionary lability of anole thermal tolerances. Across the native anoles of the Greater Antilles, thermal biology traits are much more evolutionarily labile than morphological traits (Hertz *et al.* 2013). A phylogenetic study of the native *cybotes* clade on Hispaniola also showed high variability in thermal niches among species; species evolved to tolerate high temperature behaviorally by augmenting the amount of time they spend basking, but evolved to tolerate lower nighttime temperatures through physiological means (Muñoz *et al.* 2014). As a result, cold tolerance has evolved across *cybotes* clade species at a faster rate than heat tolerance.

It is clear that native anoles exhibit substantial trait adaptation in response to environmental conditions such as temperature and vegetation structure. However, the mechanisms, genetic and otherwise, behind these adaptations and the speed with which these adaptations occurred are poorly understood. Given that both experimentally and unintentionally introduced populations from multiple anole species exhibit rapid adaptation to novel environmental conditions (Table 2), studying the spread of exotic anoles

should provide new insight into the adaptation process of colonizing species.

SPECIES INTERACTIONS

Species interactions, namely competition, have been an important source of selective pressure on anole functional traits as well as a major force in structuring species distribution patterns. Anoles compete strongly over prey and partition thermal and structural microhabitats (e.g., Schoener 1968). As ecological trait similarity between species increases, the strength of competition increases (see Losos 2009 for a review of the data on anole interspecific competition). For example, on St. Martin, the two native species (*Anolis pogus* and *Anolis gingivinus*) are more similar in size and ecological traits than the two native species on St. Eustatius (*Anolis schwartzi* and *Anolis bimaculatus*). In a set of experiments, Pacala and Roughgarden (1982, 1985), measured the pair-wise strength of competition between the more similar anoles on St. Martin and replicated the experiment for the two more divergent species on St. Eustatius. Because *A. pogus* and *A. gingivinus* on St. Martin have more similar body size and foraging behavior, they exhibited stronger competition: growth rates and fecundity were reduced when *A. gingivinus* was experimentally raised with *A. pogus*, while no negative effects were seen when *A. bimaculatus* was raised with *A. schwartzi*. Present-day coexistence of the ecologically similar *A. pogus* with *A. gingivinus* might be facilitated by the competitively dominant *A. gingivinus* having a higher susceptibility to lizard malaria (Schall 1992).

Strong competition between species with similar traits is likely responsible for consistent body-size distribution patterns across the Lesser Antilles. Like St. Eustatius, eight other major Lesser Antilles islands have one large and one small native species (Schoener 1970). This divergence in body size between the two species is likely due to competitive exclusion and character displacement (Giannasi *et al.* 2000; Losos 2009; Miles & Dunham 1996). The hypothesis is that only species with traits dissimilar to the traits of the resident species could successfully colonize the islands by avoiding competitive exclusion. Meaning, if a large anole species colonized first, only a small anole species could successfully colonize afterward. Following establishment, character displacement most likely occurred in a few instances to further reduce interspecific competition.

Comparatively, the majority of islands in the Lesser Antilles have only one intermediate-sized anole species. Intermediate-size is predicted to be the optimal size for anoles based on the size distributions of their prey (Roughgarden & Fuentes 1977; Schoener 1969b). If intermediate size is optimal, intermediate-sized anoles likely successfully outcompete smaller and larger colonists resulting in a single, intermediate-sized species on these islands.

Because competition is likely a major mechanism limiting the colonization success of anoles that disperse naturally, competition with resident species should also prevent the establishment of exotic anole species (i.e., biotic resistance). Indeed, there is evidence that it is less likely for exotic anoles to establish on those islands that have ecologically similar native species (Losos *et al.* 1993). Theoretically, exotic anoles that successfully establish should have different traits than resident species to avoid competition, or if the exotic and resident species have similar traits, the exotic must be a superior competitor. Empirically, there is support for both scenarios.

In several examples, exotics and/or natives have altered behavioral and morphological traits to reduce interactions. For example, on small intracoastal waterway islands in Florida where *A. sagrei* recently invaded, the native *A. carolinensis* now forages higher in the canopy away from the lower foraging *A. sagrei*. As a result of this behavioral shift, *A. carolinensis* has evolved larger toepads that improve clinging ability (Stuart *et al.* 2014). Similarly, the native *Anolis conspersus* on Grand Cayman has shifted to perch higher when sympatric with the introduced *A. sagrei* (Losos *et al.* 1993). In south Florida, exotic populations of *A. cristatellus* that are sympatric with exotic populations of *A. sagrei* have shorter, broader, and deeper heads (Losin 2012). As head shape strongly influences prey consumption, these differences in *A. cristatellus* head shape are consistent with interspecific competition from *A. sagrei*, driving ecological character displacement. Rapid change in behavioral and morphological traits may facilitate niche partitioning in order to reduce competition, allowing exotics and natives to coexist sympatrically, similar to the partitioning seen among sympatric native anoles (e.g., Schoener 1968).

While there are certainly examples of exotic anoles coexisting sympatrically with natives and other exotics, competitive exclusion also occurs. The exotic *A. cristatellus* on Dominica is competitively displacing the native *A. oculatus* from natural habitats (Eales *et al.*

2010; Malhotra *et al.* 2011). On Trinidad, *Anolis aeneus*, an exotic from Grenada, may competitively displace *A. trinitatis*, an exotic from St. Vincent, from degraded forest habitats (Hailey *et al.* 2009). An experimental introduction of *A. pogus* to Anguillita was not successful presumably due to competition from the native *A. gingivinus* (Roughgarden *et al.* 1984), and competition from *A. gingivinus* may have been responsible for the failed introduction of *A. bimaculatus* on St. Martin (Powell *et al.* 2011)—although evidence for competitive exclusion causing these failed introductions is arguably weak.

While competition is likely a strong force influencing both native and exotic anole establishment success, we have less of an understanding of how predation has influenced native and exotic anoles on ecological and evolutionary timescales. Native communities can exert biotic resistance in the form of consumer–resource interactions (e.g., predation and parasitism) on invading species, although this mechanism has received little research attention with respect to anoles. The exotic anoles in Trinidad provide a hint that predation-based biotic resistance may be operating. The two exotics, *A. trinitatis* and *A. aeneus*, are not found in intact forest habitat, and it has been suggested that this is due to high predation rates in natural Trinidadian forests (Hailey *et al.* 2009; Holt 1977). The few reports of predation on exotic anoles include the mountain wolf snake in Taiwan eating *A. sagrei* (Norval *et al.* 2007), the endangered Ogasawara buzzard eating *A. carolinensis* in the Bonin Islands near Japan (Kato & Suzuki 2005), and exotic *A. equestris* from Cuba eating exotic *A. distichus* from Hispaniola in Florida (Stroud 2013). *Anolis* antipredator defenses are largely behavioral (Leal & Rodríguez-Robles 1995); therefore, the main natural predators of anoles such as snakes, birds, and lizards may be preadapted to predate exotic anoles where exotics and natives co-occur. However, in regions like Asia where anoles are not endemic, predators must learn how to consume novel anole prey.

If native species are able to resist exotic anole establishment, then this biotic resistance should work best in environments that are intact where native competitors and predators are well-established and fill native niche space. On many islands, exotic anoles are absent from intact native habitats and are only found in anthropogenically altered habitats. Superficially, this pattern matches the outcome of biotic resistance; however, other factors such as altered microclimates and limited dispersal may be at play. For example, on Aruba

the Cuban green anole, *Anolis porcatius*, a species that requires humid microclimates, was likely introduced in a shipment of coconut palm trees planted in a resort garden (Odum & Van Buurt 2009). Resort gardens often contain exotic plant species and irrigation, which makes them highly divergent from native habitats. While *A. porcatius* is well established in the artificial habitat of the irrigated garden, it is absent from the arid natural environment of Aruba where the native *Anolis lineatus* thrives. On St. Martin, the exotic *A. cristatellus* has been on the island for years, but relegated to only a resort garden (Yokoyama 2012; Jesse unpublished data). In this case, the microclimates in the resort garden are more similar to those of the native habitat, yet the garden is isolated by inhospitable habitat (e.g., parking lots and buildings) likely limiting the dispersal of *A. cristatellus* to the native habitat.

Exotic colonization success through both character displacement and competitive exclusion of natives occurs, yet the strength and influence of competition has not been explicitly measured for most all sympatric exotic and native anole species. Further work is necessary to elucidate the role of predation in anole evolution and whether predation limited the establishment success of naturally colonizing anoles in the past and exotic anoles in the present. It is also clear that more data, and finer tests, are needed to quantify the role of biotic resistance in halting exotic establishments, although correlative data do suggest that failed exotic colonizations occur most frequently on islands with ecologically similar native anoles (Losos *et al.* 1993). However, the naturalization of exotic anoles into novel anthropogenic habitat must be accounted for when presenting evidence for biotic resistance.

ANOLE ECOMORPHS

One of the most remarkable outcomes of adaptation to environmental variation and species interactions is the convergent evolution of six distinct habitat specialist “ecomorphs” that have evolved repeatedly and independently across the Greater Antilles islands (Losos 2009; Mahler *et al.* 2013; Williams 1983). Classification of anole species into particular ecomorph categories is based on morphological traits, behavior, and habitat use. For example, species from the “trunk-crown” ecomorph have elongated bodies with relatively short fore- and hind-limbs, and larger toepads, which allow them to maneuver efficiently on

narrow diameter branches in the canopy; while species from the “trunk-ground” ecomorph have longer hindlimbs that allow them to run faster on thicker diameter branches. The six ecomorphs partition resources in a manner that reduces interspecific competition among sympatric species. When two species from the same ecomorph category are sympatric, they partition resources more finely by either exploiting different climatic microhabitats, or differing substantially in body size (see the review in Losos 2009).

Ecomorphs have not evolved on the Lesser Antilles islands; however, many species are morphologically comparable to the trunk-crown ecomorph (Losos & de Queiroz 1997). In some cases, intraspecific trait variation is higher in Lesser Antilles species than Greater Antilles species. For example, *A. oculatus* from Dominica exhibits substantial interpopulation differentiation whereby different populations can be classified as either trunk-ground or trunk-crown ecomorphs (Knox *et al.* 2001). Comparatively, no Greater Antilles species can be classified into more than one ecomorph category. Further, in the Bahamas, intraspecific trait variation in limb length for *A. sagrei* follows the same phenotypic pattern as ecomorphs but to a lesser degree: *A. sagrei* populations that use broader diameter perches have longer limbs than those using smaller diameter perches (Calsbeek *et al.* 2007).

There is no clear pattern with respect to geographic origin or ecomorph category that predicts exotic success. Of the 22 exotic anole species, 12 are evolutionarily derived from the Greater Antilles, 9 are from the Lesser Antilles, and 1 is derived from a mainland South American clade (Table 1). Six exotic species are trunk-crown ecomorphs, three are trunk-ground ecomorphs, two are crown-giant ecomorphs, and one is a trunk ecomorph. There are currently no twig or grass-bush species that have exotic populations. While, as previously discussed, there is certainly evidence that particular traits make it more likely for some species to become good exotic colonizers over others (Latella *et al.* 2011; Poe *et al.* 2011), there is not a strong pattern of some ecomorphs establishing more than others (Table 1).

The absence of a consistent pattern in the ecomorphology of exotic anoles may be the result of a different phenomenon: islands once depauperate in particular ecomorphs are now acquiring them. Cayman Brac originally lacked the trunk-crown ecomorph, but now the exotic trunk-crown *Anolis maynardi* is widely established on the island. In the reverse, Grand Cayman

naturally has the trunk-crown ecomorph (*A. conspersus*), but lacked a trunk-ground species until *A. sagrei* established. Note that neither of these island’s single native anoles, *Anolis luteosignifer* on Cayman Brac and *A. conspersus* on Grand Cayman, exhibits ecological release such that they have high trait variation and are found in multiple habitats. Instead, the ecomorphology of each native has diverged little from their ancestor clades: the trunk-ground *sagrei* clade of Cuba in the case of *A. luteosignifer* and the trunk-crown *A. grahmi* clade of Jamaica in the case of *A. conspersus*. This evolutionary conservatism seems to allow for the invasion of other ecomorphs. As a nuanced example, Jamaica already had a native trunk-ground ecomorph, *Anolis lineatopus*, when trunk-ground *A. sagrei* invaded, yet the two seem to coexist on the island perhaps due to habitat partitioning where *A. lineatopus* prefers shaded forests and *A. sagrei* dominates open areas where other native Jamaican anoles are not found (Lister 1976; Williams 1969).

Will this trend of adding new ecomorphs to islands that previously lacked them continue? Jamaica, for example, still does not have a trunk ecomorph, but the exotic *A. distichus* from Hispaniola is a trunk ecomorph that is established in Florida. With the large amount of trade between the United States and Jamaica, will *A. distichus* from the United States eventually establish a Jamaican population? Or perhaps *A. distichus* from its native range in the Bahamas or Hispaniola will eventually be transported to Jamaica.

BIOGEOGRAPHY OF ANOLES IN THE ANTHROPOCENE

While it is clear that exotic anoles can successfully survive human-assisted translocation and adapt to novel conditions, a major challenge is to understand how biogeographic patterns have been altered in the Anthropocene. The equilibrium theory of island biogeography proposes that as islands become more saturated with species, competitive interactions increase, which causes extinction rates to increase (MacArthur & Wilson 1967). As a result, it is less likely for a colonizing species to establish and spread on an island with many resident species given its area (i.e., a saturated island). The spread of exotic anoles in the Caribbean matches this expectation: the least saturated island banks (i.e., banks with the fewest native species given their area) have had the most exotic anoles

colonize (Helmus *et al.* 2014). The least saturated banks are those that are geographically isolated and that have not had cladogenic (*in situ*) speciation (Losos & Schluter 2000).

This filling of the unsaturated island banks with exotic anoles has strengthened the relationship between anole species richness and area across Caribbean island banks. In the past, the relationship was two part—species richness rose modestly up to a threshold area where cladogenic speciation occurred, and then rose rapidly with increasing area. This two-part relationship is thought to be due to how area regulates speciation: small islands are not large enough for allopatric speciation, which drives the accumulation of anole species richness on the large islands (Losos & Schluter 2000). However, in the Anthropocene, the establishment of exotics on the least saturated banks has caused the Caribbean anole species–area relationship to become linear. In the past, there was also a strongly negative species–isolation relationship because the most geographically isolated banks were the least saturated, but today the negative relationship has been almost eliminated. Now it is the economic isolation of island banks (e.g., number of cargo ships docking), not geographic isolation, that determines anole colonization rates in the Anthropocene (Helmus *et al.* 2014).

In the past, Caribbean banks contained closely related species (i.e., low phylogenetic diversity) because anole species naturally accumulated through ancestral colonizations from proximate banks followed by cladogenic speciation on the larger banks (Fig. 3a; Helmus & Ives 2012; Helmus *et al.* 2014; Losos & Schluter 2000; Mahler *et al.* 2010; Thorpe *et al.* 2004). These geographic constraints also caused native anoles from the same bank to be more closely related to each other than expected if species had randomly colonized banks regardless of geographic location (Fig. 3b). In the Anthropocene, anole phylogenetic diversity is accumulating rapidly because exotic anoles are able to invade geographically distant banks that contain distantly related anoles. As a result, the total amount of evolutionary history encompassed on average by species on a Caribbean bank (i.e., both natives and exotics combined) has risen by approximately 70 million years, a 25% increase in anole evolutionary history since European settlement of the Caribbean (Fig. 3a). Anole assemblages are also more phylogenetically random, because the exotics that colonize banks come from across the Caribbean and are also distributed

widely across the *Anolis* phylogenetic tree, as opposed to all being from the same clade (Fig. 3b; Helmus *et al.* 2014).

What are the ecological consequences of increased phylogenetic diversity and randomizing anole species composition? When phylogenetically distantly related species have different traits than residents, they may be more likely to become invasive when introduced (Strauss *et al.* 2006). Therefore, the ecological consequences of *Anolis* introductions are likely a function of the traits of the resident and exotic species involved (Losos *et al.* 1993; Poe 2014). However, it is not a given that distantly related species have different traits; there is considerable trait convergence across the *Anolis* tree (Mahler *et al.* 2013). If an exotic does have different traits than the resident species, it may be at an advantage. However, there are likely far more exotic introductions than colonizations, and the species that successfully colonize likely have the traits necessary to survive in a particular island environment, which are also likely the same traits as the native species. Clearly, more work is necessary to explore the mechanisms and consequences of the pattern of increased phylogenetic diversity and randomized anole composition.

CONCLUSION

We contrasted the ecology and evolution of exotic anoles with that of native anoles (Table 2). One of the strongest patterns we found is that exotics often contain more evolutionary history—in terms of within-population genetic diversity and among-species phylogenetic diversity—than native anoles (Figs. 2, 3). Genetic diversity is higher in exotics because many exotic populations are derived from admixture of multiple colonizations from genetically distinct native range sources. Phylogenetic diversity of anole assemblages is increasing on Caribbean banks because exotic anoles are transported from geographically distant areas. This means that any given exotic anole that colonizes a Caribbean island is likely distantly related to the native anoles of the island. In the Anthropocene, the evolutionary history encompassed by anole populations and assemblages is increasing due to exotic anole colonizations.

Other patterns are also emerging (Table 2). Those natives that in the past were good at naturally colonizing and establishing in new areas are those best able to take advantage of human-aided dispersal in the

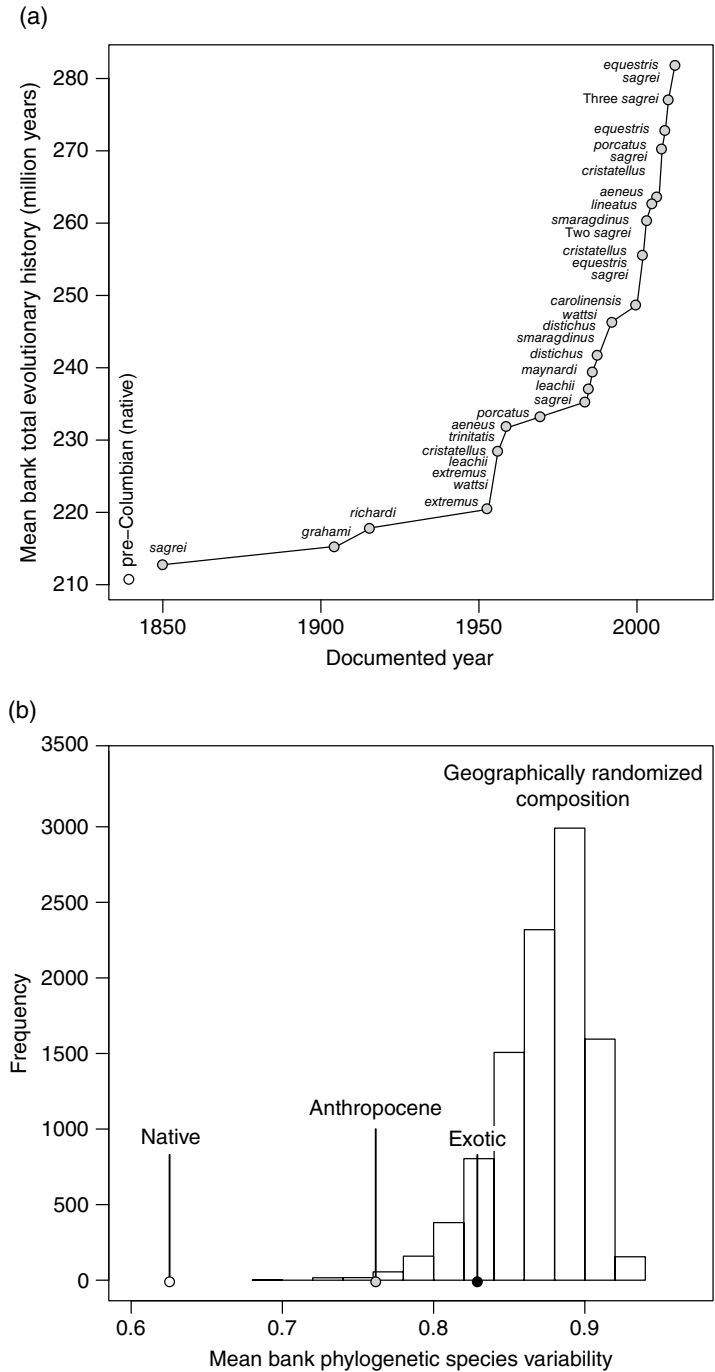


Fig. 3 Caribbean anole phylogenetic diversity is increasing in the Anthropocene. (a) The total evolutionary history of anoles on Caribbean banks (sum of phylogenetic branch lengths of species on a bank) has increased on average by approximately 25% since pre-Columbian times (also see Fig. 3 in Helmus *et al.* 2014). Points are the mean phylogenetic diversity across all Caribbean banks for a given year. Labels indicate the species that were introduced each year. Documented year is plotted because there is debate as to the actual year of some introductions. (b) Native phylogenetic species variability (average relatedness of anole species on a bank, Helmus & Ives 2012) is significantly less than expected if species randomly colonized banks regardless of geographic location ($P \ll 0.001$), while exotic anole phylogenetic composition is not ($P > 0.05$). In the Anthropocene, overall island bank composition (natives and exotics combined) is becoming less geographically structured, but still significant ($P < 0.01$). The null model histogram is of 10 000 mean values from permutations of native species among banks regardless of geographic location, but keeping the observed native bank richness constant.

Anthropocene. Exotic anoles can rapidly adapt and acclimate to new environments and species interactions, and these responses are similar to native species that are also good natural colonizers. Furthermore, native and exotics can coexist due to niche differences, phenotypic plasticity (e.g., behavioral responses), and character displacement. Islands that in the past did not contain particular ecomorphs of anoles are now gaining them. However, there is some evidence of competitive displacement of natives by naturalized exotics, and of biotic resistance of exotics by native anoles and native predators.

While native and exotic anoles can quickly adjust to new environmental conditions, the underlying architecture of genes responsible for traits related to ecological performance is unknown in many cases (Schneider 2008). Although the *Anolis* group is a well-known model system for adaptive radiation, it lags behind other adaptive radiation model systems, in part due to the comparative difficulty of rearing *Anolis* in captivity. However, the recent sequencing of the *A. carolinensis* genome (Alföldi *et al.* 2011) promises new discoveries of the genetic basis of ecologically relevant traits in the near future.

The massive introduction and naturalization of anole species in the Caribbean and across the planet is still in its exponential phase of increase and major questions remain unanswered. How will the increased genetic variation associated with Anthropocene colonizations shape future anole ecology and evolution? In the Lesser Antilles, will the islands that gained more exotic species be able to support them and maintain a higher number of species than before? Or will these islands eventually revert back to being one or two species islands? In the Greater Antilles, questions remain about ecomorph patterns. For example, Jamaica originally had only four of the six ecomorphs. Can it support all six or do some characteristics of the island limit it to only four? While we have focused on the Caribbean, what will be the eventual outcomes of those exotic anole species residing outside of the Caribbean in habitats without native anoles? Do these exotics exhibit more ecological release than exotic anoles in the Caribbean? Finally, the outcomes of these macroevolutionary questions depend largely on the magnitude of anthropogenic activities. If the translocation of species continues, island faunas may never reach an equilibrium point and could remain artificially elevated well into the future. Conversely, as humans alter the quality of habitats on islands, more invasions may be facili-

tated while simultaneously eliminating native species. One of the only certainties is that future island faunas will be the ones most tolerant to human activities.

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