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Genetic reconstruction of the invasion history of *Anolis wattsi* in Trinidad with a comment on the importance of ecological similarity to invasion success

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Human activities have reshaped patterns of island biogeography for many groups of amphibians and reptiles. In Trinidad, an island in the West Indies with only one native *Anolis* lizard species, four additional anole species have been introduced since the 1800s. The most recent introduction, *Anolis wattsi*, native to Antigua, has become established despite the presence of multiple species of resident anoles. We used genetic data (mitochondrial DNA) to infer the geographic origin and genetic structure of introduced *A. wattsi* on Trinidad. We then gathered published data to compare eco-morphological traits of all anole species currently established on the island. We found three mtDNA haplotypes in Trinidad that clustered with two different clades from the northern part of the native range in Antigua, rejecting the hypothesis that the lizards originated in the pineapple-growing region of the south. However, a lack of fine-scale population structure precluded precise identification of the origin in Antigua of haplotypes introduced to Trinidad. Compared to the other anole species on Trinidad, *A. wattsi* is smaller, perches lower, and has a higher field body temperature. Thus, the successful establishment and spread of *A. wattsi* should not be surprising given the success of two previous introductions of anole species that were more similar eco-morphologically to the native species and each other, and the fact that Trinidad has relatively few anole species for its size.

Keywords: Anolis lizards; Caribbean islands; eco-morphological traits; invasions; mtDNA

INTRODUCTION

In the Anthropocene epoch, islands and mainland coastal regions are hotspots of established non-native species (Dawson et al., 2017) and human-aided introductions have reshaped species-area and species-isolation relationships (Sax et al., 2002; Helmus et al., 2014). Although successful invasions have certainly altered biogeographic patterns for *Anolis* lizards in the Caribbean (Helmus et al., 2014), we know relatively little about the process of transport, establishment and spread for these invading anole species. Genetic analyses can be used to better understand the pathways for introduction and spread of non-native anoles (e.g. Kolbe et al., 2004; 2007) and comparisons of ecological similarity to native species may be useful for predicting the outcome of these novel interactions (Losos et al., 1993) and their potential ecological impact on native communities.

Species co-existence in *Anolis* lizards is strongly influenced by their position on three ecological niche axes; structural microhabitat (e.g. perch diameter and height), thermal microhabitat, and body size, which influences both diet and interspecific interactions (Losos, 2009). Greater ecological similarity on these niche axes should increase the strength of interspecific competition (Roughgarden, 1995) and may limit successful establishment of introduced species. Indeed, a previous study found that *Anolis* lizard introductions were more successful when resident and invading species were ecologically different; a designation based primarily on ecomorph (or habitat specialist) groups for Greater Antillean species and body-size differences for Lesser Antillean species (Losos et al., 1993). However, this type of categorical assessment of ecological similarity lacks the detail needed to identify which niche axes might limit coexistence and precludes evaluation of the role of ecological and evolutionary trait change during the invasion (Kolbe et al., 2012; Stuart et al., 2014).

Trinidad is by far the largest island in the Caribbean with only one native *Anolis* species, *A. planiceps* (formerly *A. chrysolepis planiceps*). Martinique, the next largest island with only one native anole species, is less than one-
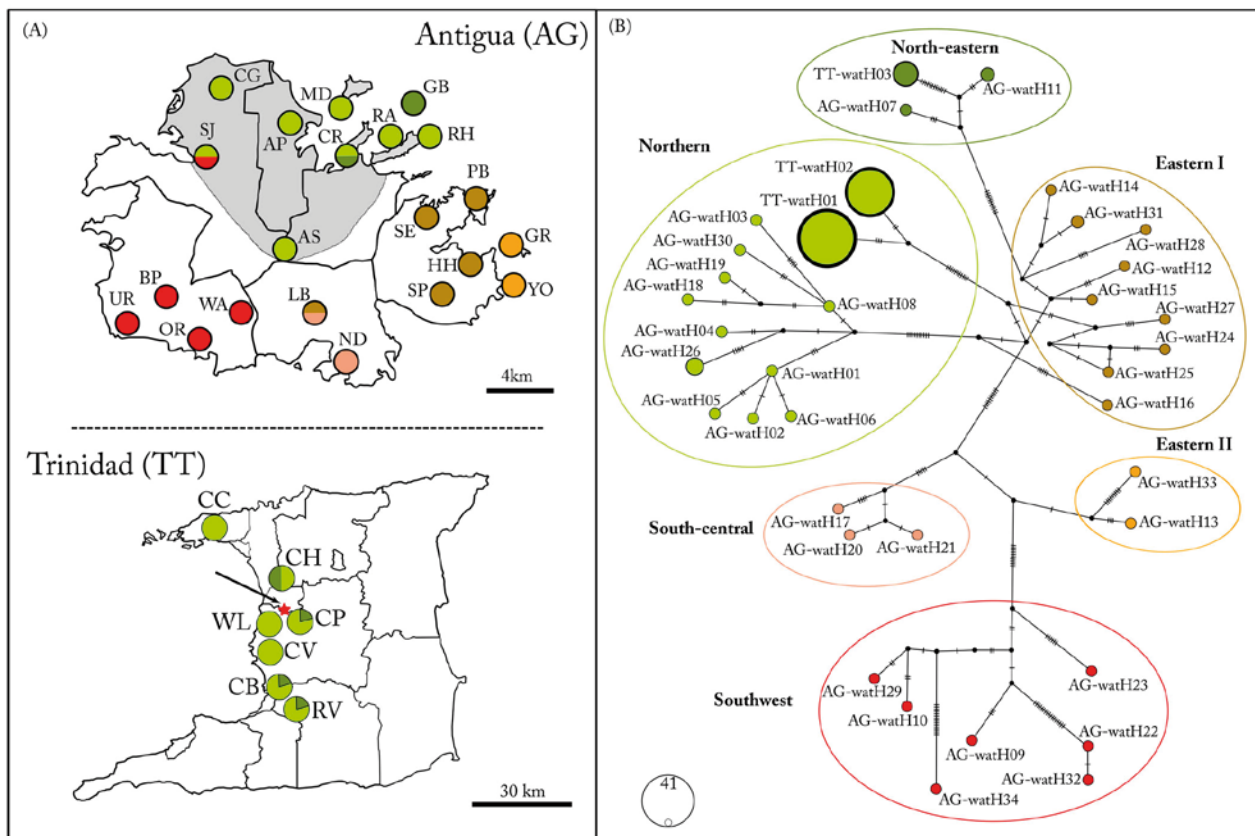
Figure 1. Sampling locations and mtDNA haplotype distribution. **(A)** Distribution of sampling locations in the native (Antigua) and introduced (Trinidad) ranges with pie charts indicating percentage of different haplogroups present. The arrow and red star show the location where lizards were first discovered at the Caroni Research Station in Trinidad. Grey-shaded area in Antigua indicates the most likely region of origin based on mtDNA haplotype divergence. **(B)** Median-joining network of 135 mtDNA ND2 sequences. The size of the pie indicates the number of individuals sharing that haplotype. The six haplogroups correspond to the mtDNA clades from the phylogenetic analysis (see Fig. S1). The three haplotypes found in Trinidad (TT-watH01, TT-watH02 and TT-watH03) group with the northern and north-eastern clades in Antigua.

quarter of its size. However, due to the high economic connectivity with other islands across the Caribbean, four exotic anoles have been introduced since the 1800s (Kraus, 2009), the highest number of introduced *Anolis* species for any island in the Caribbean. The first non-native anole to establish on Trinidad was *A. aeneus*, previously endemic to Grenada, and currently the most abundant anole in suburban gardens (White & Hailey, 2006). *Anolis trinitatis*, previously endemic to St Vincent, is another naturalised species in Trinidad, whereas *A. extremus* from Barbados is now considered extirpated despite multiple introduction attempts since the 1960s (White & Hailey, 2006). The most recent introduction was *A. wattsi*, native to Antigua. The co-occurrence of ecologically similar anole species on Trinidad provides an opportunity to assess the predictive power of ecological similarity for the establishment, spread and ecological impact of invasive species.

Anolis wattsi* was first discovered in 1992 on the grounds of Caroni Research Station in Waterloo (Fig. 1, Boos, 1996; White & Hailey, 2006). Because the lizards were spotted on pineapple plants (cultivar "Black Antigua"), it has been suggested that planting material shipped from south-western Antigua was the likely source of the population (White & Hailey, 2006). However, a thorough survey by White & Hailey (2006) found no direct evidence that the introduction was on pineapple plants. In addition, relatively early accounts of lizards at an import/export terminal of a cement factory in Claxton Bay, Trinidad (CB, Fig. 1), approximately 15 km south of Waterloo (WL, Fig. 1), could have been another site of introduction (White & Hailey, 2006). Consequently, the source and the timing of the introduction remain unresolved, which limits our ability to compare non-native populations to their native-range source. Furthermore, following its localised establishment in west-central Trinidad, the species is currently found in at least seven localities (White & Hailey, 2006). Their discontinuous distribution, separated by presumably unfavorable habitat (i.e., areas of sugar cane cultivation) suggests establishment through jump dispersal (*A. Hailey*, unpubl. data; White & Hailey, 2006), however, testing these hypotheses requires extensive sampling and analysis of genetic data.

In this study, we first used phylogenetic and population-genetic analyses of mitochondrial DNA (mtDNA) sequences to infer the geographic source (origin) and genetic structure of introduced *A. wattsi* populations on Trinidad. We then gathered published data of eco-morphological traits to compare all resident

anole species in Trinidad and evaluate the importance of ecological similarity for invasion success.

MATERIALS AND METHODS

Genetic analyses

We sampled 95 adult *A. wattsi* from seven locations on Trinidad (Fig. 1, Table 1) and 39 from the native range in Antigua (20 locations, Fig. 1, Table 1). We sequenced an approximately 1200 base pair (bp) region of mitochondrial DNA including the ND2 gene for all individuals and used Bayesian inference and median-joining network analysis to reconstruct phylogenetic relationships among haplotypes and assign non-native range haplotypes to their geographic origin in the native range (detailed protocol in Supplementary Material). We calculated nucleotide diversity (Pi) per sampling location in DNAsp v.6 (Rozas et al., 2017) and compared Pi in native versus non-native range with a Welch Two Sample *t*-test in R v3 (R Development Core Team 2017). For this comparison, we excluded two locations in the native range where only one sample was collected.

Eco-morphological similarity

We collected data from the literature to determine whether each introduced anole species in Trinidad was ecologically similar to the resident species preceding their introduction. We included data on body size (maximum male snout to vent length, SVL), hind-limb length (HLL), head length (HDL), and field active body temperature (Tb) as well as the mean, niche breadth (NB) and niche overlap (NO) for aspects of structural microhabitat use (i.e., substrate, perch height and perch diameter).

RESULTS

Our analyses of sequences from 134 individuals identified 36 haplotypes (GenBank accession numbers MH375645-MH375680), 33 in the native range of Antigua and three in the introduced range of Trinidad. No haplotypes were shared between Antigua and Trinidad, and introduced-range haplotypes showed considerable nucleotide divergence (1.2-1.4 %) from the closest native-range haplotypes. Two haplotypes (TT-watH01 and TT-watH02) represented 85 % of the individuals sampled in the

Table 1. Details on sampling locations with mtDNA haplotypes identified.

Island	Locality	Abbreviation	Date$	Ns	Haplotype*
Trinidad	Claxton Bay	CB	2003	10	TT-watH01(3), TT-watH02(6), TT-watH03(1)
Trinidad	Cocorite	CC	2005	10	TT-watH02(10)
Trinidad	Charlieville	CH	2008	20	TT-watH01(10), TT-watH03(10)
Trinidad	Carapichaima	CP	2004	15	TT-watH01(6), TT-watH02(7), TT-watH03(2)
Trinidad	Couva	CV	2004	10	TT-watH01(4), TT-watH02(6)
Trinidad	Reform Village	RV	2005	10	TT-watH02(9), TT-watH03(1)
Trinidad	Waterloo	WL	1992	20	TT-watH01(18), TT-watH02(2)
Antigua	Airport	AP	-	2	AG-watH01, AG-watH02
Antigua	All Saints	AS	-	2	AG-watH03, AG-watH04
Antigua	Cedar Grove	CG	-	2	AG-watH05, AG-watH06
Antigua	Crabbs Peninsula	CR	-	2	AG-watH07, AG-watH08
Antigua	Urlings	UR	-	2	AG-watH09, AG-watH10
Antigua	Great Bird Island	GB	-	2	AG-watH11(2)
Antigua	Green Island	GR	-	2	AG-watH12, AG-watH13
Antigua	Harmony Hall	HH	-	2	AG-watH14, AG-watH15
Antigua	Liberta	LB	-	2	AG-watH16, AG-watH17
Antigua	Maiden	MD	-	2	AG-watH18, AG-watH19
Antigua	Nelson's Dockyard	ND	-	2	AG-watH20, AG-watH21
Antigua	Old Road	OR	-	2	AG-watH22, AG-watH23
Antigua	Pineapple Beach	PB	-	2	AG-watH24, AG-watH25
Antigua	Rabbit Island	RA	-	2	AG-watH26(2)
Antigua	Red Head Island	RH	-	2	AG-watH26(2)
Antigua	Seatons	SE	-	2	AG-watH27, AG-watH28
Antigua	St John's	SJ	-	2	AG-watH29, AG-watH30
Antigua	St Philips	SP	-	2	AG-watH31(2)
Antigua	Wallings	WA	-	1	AG-watH32
Antigua	York	YO	-	2	AG-watH33(2)
Antigua	Boggy Peak	BP	-	1	AG-watH34[#]

$ Date first documented/observed * Number in parenthesis corresponds to the number of individuals sharing that haplotype.
[#] AG-watH34 corresponds to a published haplotype (Jackman et al., 1999) with GenBank accession number AF055931

Table 2. Summary statistics for mtDNA haplotype variation for the native and non-native ranges of *A. wattsi*. Number of sampling locations (Nl), number of individuals sampled (Ns), number of haplotypes identified (Nh) and nucleotide diversity (percentage, Pi).

Range	Island	Nl	Ns	Nh	Pi (%)
Native	Antigua	21	40	34	0.69
Non-native	Trinidad	7	95	3	0.42

introduced range and these haplotypes differed by five nucleotides (0.4 %) from each other and 1.8-2.1 % from TT-watH03 (Table 1).

The phylogenetic analysis supported a well-resolved topology with six geographically distributed clades in Antigua (two northern clades, two eastern clades, a south-central clade and a south-west clade, Fig. S1). The introduced haplotype TT-watH03 was nested within the Northern clade I and haplotypes TT-watH01 and TT-watH02 were nested within the Northern clade II (Fig. 1B). Four localities in Trinidad (CH, CP, CB and RV) contained haplotypes from both of these native-range clades (Fig. 1A). In addition, three locations in Antigua (SJ, CR and LB) contained haplotypes belonging to different combinations of two different clades (Fig. 1A). Nucleotide diversity (Pi) was lower in the introduced range compared to the native range (Table 2), albeit not significantly (t = -1.19, df = 21.75, P = 0.25).

Eco-morphological traits varied in similarity between pairs of introduced species in Trinidad (Table 3). In all instances, morphological and structural habitat values were greater in the older-established anoles, *A. aeneus* and *A. trinitatis*. Structural niche breadth (in all three dimensions; substrate, perch height, perch diameter) was generally greater in *A. aeneus* and *A. trinitatis* compared to *A. wattsi*, and both of these anole species perched on higher and broader vegetation compared to *A. wattsi*. Niche overlap for substrate (NO-S) was lower between *A. aeneus* and *A. wattsi* (NO-S = 0.666, Table 4) compared to *A. aeneus* and *A. trinitatis* (NO-S = 0.990, Table 4). Perch diameter overlap was high between both pairs; *A. aeneus* and *A. trinitatis* (NO-PD = 0.995) and *A. aeneus* and *A. wattsi* (NO-PD = 0.97). Perch height overlap was lower between *A. aeneus* and *A. wattsi* (NO-PD = 0.839) compared to *A. aeneus* and *A. trinitatis* (NO-PD = 0.997). Finally, body size ratio was 1.43 or less for all pairs (Table 4), well below the ratio of 1.65 for co-existing native Lesser Antilles anoles (Losos 2009).

DISCUSSION

In this study, we first used mtDNA sequences to infer the geographic origin and genetic structure of introduced *A. wattsi* and investigate their patchy distribution on Trinidad. We found three haplotypes in the non-native range that are closely related to native-range haplotypes from the northern part of Antigua around Crabbs peninsula. Presence of haplotypes from two different native-range clades in four out of seven non-native populations suggests the possibility of multiple

introductions and admixture. However, this did not lead to increased genetic diversity in terms of the numbers of haplotypes and nucleotide diversity within non-native populations as found in some other *Anolis* invasions (Kolbe et al., 2004, 2007; Michaelides et al., 2018). We discuss these results and the importance of ecological similarity to invasion success.

The phylogeographic history of a species in its native range determines the distribution of genetic diversity available from which colonists are drawn and only strong phylogeographic structure in the native range can support precise identification of the source locations (Taylor & Keller, 2007). In Antigua, the native range of *A. wattsi*, there is weak to moderate geographic structure. Given our geographically widespread sampling, it is somewhat surprising that we did not find the same or very similar haplotypes to those in Trinidad, which could suggest an origin from a location in Antigua that was not sampled. The closest native-range haplotypes are from the northern part of the island including several offshore islands: the airport, Crabbs peninsula, St John's, and Cedar Grove, which has a large nursery. Interestingly, Crabbs peninsula contains haplotypes from both northern clades similar to four out of seven locations in Trinidad with 1.2-1.4 % sequence divergence from all introduced haplotypes. The first location of *A. wattsi* in Trinidad at an agricultural research station suggests importation on live plant material, particularly pineapples. However, our genetic data reject the earlier hypothesis regarding the source being a location in the south-western part of Antigua (where a major pineapple farm is based), and support a more likely source somewhere in the vicinity of Crabbs peninsula, which is near a shipping port in the northern part of Antigua.

Lizards were first discovered in Trinidad at the Caroni Research Station, in Waterloo, which was also suspected to be the initial point of introduction. However, only two out of the three haplotypes were found there (TT-watH01 in higher frequency than TT-watH02), whereas in Carapichaima, which is less than a kilometer to the east, all three haplotypes are present (but only two out of 15 individuals have the third haplotype TT-watH03). The absence of TT-watH03 from Waterloo, and the low frequency overall across Trinidad, could be a result of a founder effect during the initial introduction. Another possibility would be that a second introduction occurred to Carapichaima either directly from Antigua or more likely from another location within Trinidad where the third haplotype also exists. For instance, Claxton Bay where all three haplotypes are also found could have been another point of introduction. This location was discovered in 2003 (White & Hailey, 2006) and could have served as another source of *A. wattsi* at other sites in Trinidad through human transport of building material. In Charlieville, about 10 km north of Waterloo, *A. wattsi* was first discovered in 2008 by The University of the West Indies technicians collecting mosquitoes (A. Hailey, unpubl. data). Interestingly, samples collected (10 individuals) on each side of the major highway there, were fixed for two different haplotypes, TT-watH01 to the east and TT-watH03 to the west (highest frequency across

Table 3. Summary of eco-morphological characteristics of native and non-native anoles in Trinidad. Body size (maximum male SVL), hind-limb length (HLL), head length (HDL), active body temperature (Tb), mean perch height (PH), mean perch diameter (PD) and niche breadth (NB) for each dimension of the structural habitat niche: substrate (NB-S), perch height (NB-PH), and perch diameter (NB-PD).

Species	Date	Native Isl.	SVL[2]	HLL[2]	HDL[2]	Tb[3]	PH (cm)[4]	PD (cm)[4]	NB-S[4]	NBPH[4]	NB-PD[4]
A. planiceps	-	Trinidad	76[5]	-	-	-	-	-	-	-	-
A. aeneus	1900	Grenada	77	16.4	17.0	31.0	83	12	4.85	4.74	3.39
A. trinitatis	1900	St Vincent	74	17.0	16.6	30.3[6]	105	14.3	3.67	4.14	4.02
A. extremus	1960	Barbados	83	-	-	-	-	-	-	-	-
A. wattsi	1992	Antigua	58	13.9	14.3	33.3	46	11	4.46	2.65	2.87

[1] Approximate date of introduction
[2] Data from Poe (2014)
[3] Data from Hertz et al. (2013)
[4] Data from Hailey et al. (2009) and White & Hailey (2006)
[5] Data for *A. planiceps* [*A. chrysolepis planiceps* from D'Angiolella et al. (2011)]
[6] Data from Gorman et al. (1971)

Table 4. Ecological similarity and current status in Trinidad. The numbers below the diagonal represent niche overlap for substrate (NO-S), and the ones above the diagonal represent body size ratio. The diagonal represents the outcome of each introduction and the current distribution in the case of the native *A. planiceps*.

Species	*A. planiceps*	*A. aeneus*	*A. trinitatis*	*A. extremus*	*A. wattsi*
A. planiceps	Forested areas	1.01	1.02	1.09	1.31
A. aeneus	-	Widespread[1]	1.04	1.07	1.32
A. trinitatis	-	0.990	Localised[2]	1.12	1.28
A. extremus	-	-	-	Extinct[2]	1.43
A. wattsi	-	0.666	-	-	Widespread[1]

[1] From White & Hailey (2006)
[2] From Hailey et al. (2009)

all sites in Trinidad) suggesting separate introductions or different histories of establishment. Jump-dispersal within Trinidad is the most likely explanation for the patchy distribution and the variation in the frequency of haplotypes across localities. For example, the northern-most sampling location in Cocorite (CC, Fig. 1) had only a single haplotype and was probably established through human-assisted transportation of individuals from a southern location. Secondary introductions within the non-native range are common in invasions to remote locations (Kolbe et al., 2004; Floerl et al., 2009; Lombaert et al., 2010); for example, the green anole, *A. carolinensis* (native to south-eastern USA), has established several populations in Pacific islands from older-established populations in the region (Michaelides et al., 2018). Interestingly, *A. wattsi* has also been introduced to another island in the southern Lesser Antilles, St Lucia in 1956 (Kraus, 2009). Given the high level of agricultural and horticultural trade among Caribbean islands (Helmus et al., 2014), the established population of *A. wattsi* in St Lucia could have served as a secondary source of the lizards in Trinidad. Nevertheless, further sampling and genetic data are needed to test this alternative hypothesis.

Introduced populations of *A. wattsi* on Trinidad had lower genetic diversity than native-range populations, however, intraspecific admixture (presence of haplotypes from two different clades was evident in 57 % of the sampling locations) may have counteracted the severity of founder effects. Indeed, multiple introductions with admixture are a common feature for many introduced *Anolis* species (Kolbe et al., 2007). For example, *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). These independent introductions, followed by admixture in the introduced range have led to higher genetic variation in the introduced range than their native counterparts, and probably assisted in their establishment and further spread (Kolbe et al., 2004).

Whereas most anole introductions fail where there is already an ecologically similar species established (Losos et al., 1993), there were four anole species in Trinidad at the time of this study, one native and three introduced (*A. extremus* is considered extirpated). Two additional *Anolis* species have been recently detected on Trinidad, *A. cristatellus* (Auguste et al., 2018) and *A. sagrei* (Auguste 2018). In the Lesser Antilles, ecological co-existence for anoles is primarily a function of body size, which generally correlates with prey size, where pairs of anole taxa usually differ in body size by a ratio of 1.65 (Losos, 2009). In Trinidad, the body size ratio is well below this threshold for all pairs, and this greater similarity in body size is predicted to lead to stronger interspecific competition. Indeed, the first two anole introductions, *A. aeneus* and *A. trinitatis*, were very ecologically similar in all three niche dimensions (i.e., body size, structural microhabitat, and thermal microhabitat). Hybridisation

along with intense competition has been suggested as the likely cause of the decline in *A. trinitatis* and its localised occurrence (Gorman et al., 1971; Hailey et al., 2009). However, the two species might have different habitat requirements (well-vegetated areas for *A. trinitatis* versus a wider range of habitats including open areas for *A. aeneus*) and thus differ in thermoregulatory ability (that of *A. aeneus* being greater) rather than body temperatures as such (Hailey et al., 2009).

The third anole introduction, *A. extremus*, is of similar size to the older-established *A. aeneus* and *A. trinitatis*, but the failure to become established was likely due to small population size (Hailey et al., 2009). The recent addition, *A. wattsi*, has become established despite the presence of *A. aeneus* in the same area and habitat. Body size difference between these two species is the greatest among all extant anole pairs in Trinidad and could have facilitated their co-existence. Differences along other niche dimensions, for example thermal biology, substrate type and perch height might be sufficient to reduce competition (White & Hailey, 2006). For example, when *A. wattsi* co-occurs with *A. leachii* (a larger anole) in its native range, it uses lower perches compared to when in allopatry (Kolbe et al., 2008). The same pattern of perching lower is found in Trinidad when in sympatry with *A. aeneus* (White & Hailey, 2006). A habitat shift in sympatric populations of anoles has been shown elsewhere; for example, between the native *A. oculatus* (used higher perches) and the invasive *A. cristatellus* (used lower perches) compared to allopatric populations of both species in Dominica (Dufour et al., 2018). Such shifts in habitat imposed by strong interspecific interactions can also drive rapid evolutionary change in native species (e.g. Stuart et al., 2014).

The native anole on Trinidad, *A. planiceps*, is the most terrestrial of the four species currently on the island as it forages on the ground but is restricted to forested areas (White & Hailey, 2006). Introduced *Anolis* have not yet moved into undisturbed areas. However, the lower perching *A. wattsi* is more likely to compete with the native *A. planiceps* than are other introduced species due to the ground-dwelling habits of the latter (Murphy, 1997; White & Hailey, 2006). Yet, higher active body temperatures for *A. wattsi* may restrict its ability to invade forested areas inhabited by *A. planiceps*. Given its depauperate native anole fauna for an island the size of Trinidad, it should not be surprising that several non-native anole species are now well established on the island. This has occurred despite some eco-morphological similarity among the native species (*A. planiceps*) and early invaders (*A. aeneus* and *A. trinitatis*). Whether the successful invasion of *A. wattsi* was facilitated by it being more eco-morphologically distinct from resident species on Trinidad will require experimental assessment or observations of the success or failure of future invasion attempts by anole species based on their ecological similarity to the current anole fauna on the island.

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