

Ecological character displacement between a native and an introduced species: the invasion of *Anolis cristatellus* in Dominica

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Species invasions are a global scourge. Nonetheless, they provide the appropriate evolutionary setting to rigorously test the role that interspecific competition plays in species evolution. The process of ecological character displacement, in which species diverge in sympatry to minimize resource use overlap, is one example. Here, we examine whether ecological character displacement occurs as the result of a species invasion and, if so, whether morphological adaptations subsequently evolve. We studied the invasion of the lizard *Anolis cristatellus* in Dominica, where the native *Anolis oculatus* occurs, and compared nine allopatric and 11 sympatric populations at two scales: across the island, where *A. cristatellus* invaded since 1998, and in the northeastern region (Calibishie), where the species arrived in 2014. Perch height and diameter, as well as body, limb and toepad traits, were measured on 593 adults. In sympatry, habitat divergence occurred rapidly but was associated with morphological divergence at the island scale only: *A. oculatus* perched higher and possessed shorter limbs, while *A. cristatellus* moved downward with associated longer limbs and, in females, fewer toepad lamellae. The different results for the two scales suggest that sympatry is too recent at Calibishie for morphological trait evolution to occur.

ADDITIONAL KEYWORDS: *Anolis* – character displacement – interspecific competition – invasion – limb – lizard – perch height.

INTRODUCTION

Invasive species are a global scourge, responsible for driving species to extinction, imperilling ecosystems and causing billions of dollars in economic damage (Parmesan, 2006; Van der Putten, 2012). Nonetheless, they do have one positive effect: in many cases, they represent inadvertent experiments of the sort that could not ethically be conducted intentionally (Tingley *et al.*, 2014).

One example is the novel juxtaposition of species with no evolutionary history of coexistence, setting the stage for a rigorous test of the theory of ecological character displacement, which proposes that initially ecologically similar species will shift resource use in sympatry to minimize competitive pressure and

subsequently will evolve to adapt to the new resource use (Brown & Wilson, 1956; Grant, 1972; Schluter, 2000; Violle *et al.*, 2011). Although the idea was proposed more than a half-century ago and is widely believed to be an important factor driving evolutionary divergence, few well-established cases have been documented (Stuart & Losos, 2013). One reason for this lack of evidence is the difficulty in conducting experiments over the appropriate ecological and evolutionary scales. Invasive species, by coming into contact with similar species with which they have no recent evolutionary history, provide inadvertent tests of the character displacement hypothesis.

Lizards in the genus *Anolis* have played an important role in the development of character displacement. A large body of evidence (reviewed in Losos, 2009) indicates that these insectivorous lizards compete interspecifically for food and partition habitats and

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resources to minimize competitive pressures. [Schoener \(1970\)](#) first proposed that character displacement was responsible for size differences among coexisting species in the Lesser Antilles, a finding subsequently bolstered by phylogenetic analyses ([Losos, 1990](#); [Butler & Losos, 1997](#); see review in [Losos, 2009](#)). [Williams \(1972, 1983\)](#) extended this reasoning to suggest that character displacement was key to the adaptive radiation of anoles, resulting in the evolution of multiple habitat specialists, termed ecomorphs. In agreement with the character displacement hypothesis, [Stuart *et al.* \(2014\)](#) showed that native anoles in Florida shifted their habitat use and evolved morphological adaptations in the presence of an invasive anole species.

Here, we examine a situation in which two ecologically similar species have been brought into coexistence by a human-caused introduction, presenting the rare opportunity to examine a possible case of character displacement as it occurs. The island of Dominica is naturally occupied by a single species of anole, *Anolis oculatus*, a generalized intermediate-sized species usually found on ground and trunk perches. Sometime around 1998, an invasive anole species appeared at the southern end of the island ([Eales, Thorpe & Malhotra, 2010](#)). *Anolis cristatellus*, native to Puerto Rico, is ecologically and morphologically very similar to the native *A. oculatus*, so much so that several scientists predicted that the species would compete strongly, possibly even leading to the extinction of the native species ([Malhotra *et al.*, 2007](#); [Daniells *et al.*, 2008](#)).

The situation in Dominica thus presents a clear test. If character displacement occurs, we would expect the two species to diverge in habitat use, followed by divergence in body, limb and toepad morphological traits when in sympatry ([Losos, 2009](#)). Moreover, because the invasive species has spread northward since its time of introduction, we can compare populations that have only recently come into contact in the region of Calibishie with those that have been coexisting for more than a decade elsewhere on the island. Finally, because the spread of *A. cristatellus* has been patchy (due to the random spread of this species along the main road), allopatric populations occur throughout the island, allowing the comparison of ecological and morphological traits in the two contexts (i.e. allopatry vs. sympatry) for the two species.

MATERIAL AND METHODS

STUDY SITES AND SPECIES

From 1 May 2016 to 9 June 2016, a total of 775 lizards (593 adults and 182 juveniles) were sampled at two spatial scales: in sites spanning the entire island and within the Calibishie region ([Fig. 1, Table 1](#)). The sampled lizards were marked with a sharpie pen, and each population was studied for two to four consecutive days (preventing the risk of resampling the same individual after shedding). All necessary research permits (Dominican Ministry of Agriculture and Fisheries,

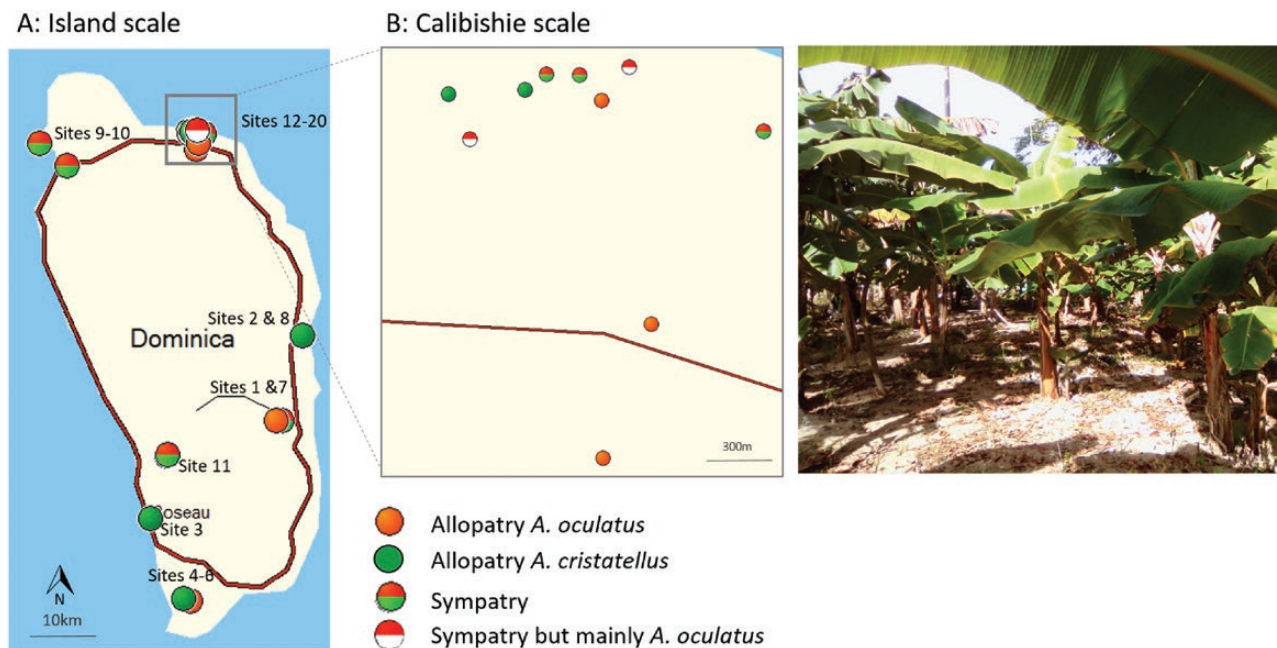


Figure 1. Distribution of the sites ([Table 1](#)) sampled across Dominica (A) with a zoom on the Calibishie region (B, with a picture of a banana farm sample site). Shading indicates context (allopatry vs. sympatry) and species sampled.

Table 1. Characteristics of studied populations at the island and Calibishie scales, according to the context, the estimated age of *Anolis cristatellus* invasion and the number of adult females and males of *A. cristatellus* and *Anolis oculatus* sampled in this study

Scale	Site	Context	<i>A. cristatellus</i> first invasion estimate	<i>A. cristatellus</i>		<i>A. oculatus</i>		Total adults
				Female	Male	Female	Male	
Island	1	Allopatry	> 2 years	0	0	14	10	24
	2		Unknown	10	9	0	0	19
	3		17–20 years	12	14	0	0	26
	4		Almost a decade	0	0	3	4	7
	5		3	6	0	0	9	
	6	Sympatry	Almost a decade	1	8	1	2	12
	7		> 2 years	6	7	8	11	32
	8		Unknown	3	9	0	4	16
	9		5	6	5	6	22	
	10		4	7	10	10	31	
	11		Almost a decade	1	3	11	8	23
Calibishie	12	Allopatry	2 years	0	0	14	33	47
	13		25	13	0	0	38	
	14		13	18	0	0	31	
	15	Sympatry	2 years	0	0	7	24	31
	16		10	11	7	14	42	
	17		1	1	12	18	32	
	18		11	14	7	21	53	
	19		11	21	6	14	52	
	20		4	3	16	23	46	

Forestry, Wildlife and Parks division) and IACUC agreements (Harvard University) were obtained to perform this study.

Long-term coexistence: island scale

In total, 221 adult lizards were sampled in 11 sites in diverse habitats (e.g. banana farms, open and closed forest, botanical gardens) across the island in areas where the species are present alone (three *A. cristatellus* and two *A. oculatus* sites) or in areas where the two species co-occur sympatrically (six sites, Table 1). For each island region studied, allopatric and sympatric sites were sampled, limiting a possible ‘region’ bias when evaluating the effect of context (Table 1).

Dating the *A. cristatellus* invasion in each area is not straightforward. Nonetheless, according to the residents and previous studies (Eales, Thorpe & Malhotra, 2008; Eales *et al.*, 2010), we can estimate the *A. cristatellus* ‘first occurrence’ date in the different populations, which ranges from a couple of years to more than a decade ago (Table 1).

Short-term coexistence: Calibishie scale

In total, 372 adult lizards were sampled in five sympatric and four allopatric sites in a standardized banana

farm habitat in the region of Calibishie (Table 1, Fig. 1). Each site was represented by a banana farm, delimited by either natural (cliff, beach and river) or artificial (road, houses) barriers. Moreover, the home range size of *Anolis* lizards is relatively small (ranging from 1.40 m² for *Anolis sagrei* to 38.20 m² for *Anolis angusticeps*; Schoener & Schoener, 1982). Thus, the distance between the sampled sites in this study (minimal distance between sites = 118 m), added to the physical barriers separating them, allowed us to treat the sites as independent for the study period. According to the information from residents, *A. cristatellus* arrived in this region no earlier than 2014.

PERCH USED MEASUREMENTS

For each sampled individual, perch height and diameter were measured to the nearest centimetre at the location where the lizard was seen for the first time during the observation period (ranging from 7:00 am to 1:00 pm).

MORPHOLOGICAL MEASUREMENTS

Each lizard was captured by noose or hand, brought to the field house for measurements and replaced at its point of capture within 10 h.

Body traits

Each individual was sexed and species identified (the two species are morphologically distinct). Body mass was measured with a Pesola scale (ACPro-200g to the nearest 0.01 g). All morphological traits were measured with a digital caliper (Mitutoyo CD-6 ASX to the 0.01 mm nearest) on the right side of the lizard. Snout-to-vent length (SVL), inter-limb length, body height and body width were measured following the protocol of Herrel, Meyers & Vanhooydonck (2001). Based on SVL, each individual was characterized as juvenile or adult (*A. cristatellus*: Fitch, Henderson & Guarisco, 1989; *A. oculatus*: Lazell, 1972).

Limb traits

For each individual, the humerus, radius, metatarsus and longest toe of the forelimb as well as the femur, tibia, metatarsus and longest toe of the hindlimb were measured with a digital caliper following the protocol of Herrel *et al.* (2001).

Foot and hand toepad area and lamella number

Pictures of the right foot and hand of each lizard were taken and scaled. Based on these pictures, the area of sub-digital pad of the fourth (longest) toe was measured with the ImageJ software following the protocol of Crandell *et al.* (2014; Supporting Information, Fig. S1); area was measured from where the next most distal lamellae is wider than the previous one to the end of the digit. The number of lamellae under the fourth toe was also recorded.

STATISTICAL ANALYSES

Statistical analysis was conducted with R-v3. (R Development Core Team, 2011). Normality and heteroscedasticity of distributions were checked by plotting the model's residuals. The significance level was set to 0.05 and adjusted for multiple comparisons with the sequential Bonferroni procedure when necessary. Separate analyses were performed for the adults from Calibishie and those of the rest of the island. For each analysis, a global model was run (with all the factors – mentioned below – and all the two- and three-way interactions) and the final model was selected based on the Akaike information criterion (AIC). When a three-way interaction was significant, three post hoc analyses (linear mixed-effect models) were performed by separating either the two species, the two contexts or the two sexes to disentangle the effect of each factor.

Perch height and diameter data were analysed with linear mixed-effect models with the context, the sex and the species (and all the two- and three-way interactions) as factors and the site as random effect.

A principal component analysis (PCA) with varimax rotation was performed on the residuals of regressions of each body and limb trait against SVL to remove body size effects. Linear mixed-effect models were performed on the first two axes (which had eigenvalues greater than one and were thus retained for further analyses) with the context, the sex and the species (and all the two and three levels of interaction) as factors and the site as random effect.

For analysis of the toepad traits, mixed-effect model was performed, with SVL as covariate; context, sex and species (and all the two- and three-way interaction) as factors; and site as random effect.

Table 2. Statistical results from the final linear mixed-effect models (based on AIC) testing the two ecological traits according to the variables (i.e. species, context, sex and all the interactions) at the island-wide and Calibishie scales

Trait	Variable	Island					Calibishie					
		Value	SE	d.f.	<i>t</i> -value	<i>P</i> -value	Value	SE	d.f.	<i>t</i> -value	<i>P</i> -value	
Ecology	Perch diameter	Intercept	2.686	0.289	205	9.287	0.000	2.649	0.111	361	23.781	0.000
		Context	-0.601	0.358	9	-1.680	0.127	0.045	0.112	7	0.404	0.698
		Species	0.647	0.183	205	3.532	< 0.001	0.235	0.101	361	2.331	0.020
		Sex	-0.066	0.147	205	-0.446	0.656	-0.212	0.094	361	-2.248	0.025
	Perch height	Intercept	4.367	0.563	204	7.759	0.000	3.862	0.272	359	14.210	0.000
		Context	-0.165	0.687	9	-0.241	0.815	-0.620	0.330	7	-1.877	0.103
		Species	-2.076	0.887	204	-2.342	0.020	-0.421	0.374	359	-1.124	0.262
		Sex	0.229	0.149	204	1.535	0.126	0.866	0.133	359	6.528	< 0.001
		Context:species	2.020	0.908	204	2.224	0.027	0.853	0.413	359	2.063	0.040

The significant results are in bold. AIC, Akaike information criterion.

RESULTS

PERCH USE

At both island and Calibishie scales, the same general pattern was observed with sympatric *A. cristatellus* perching lower and *A. oculatus* perching higher compared to allopatric context (context:species significant effect; Table 2, Fig. 2). At the island scale, the interaction between context and species on perch height is due to *A. oculatus* using significantly higher perches in sympatry (contrast Tukey: d.f. = 9, $t = -2.327$, $P = 0.044$), while the habitat shift is not significant for *A. cristatellus* (contrast Tukey: d.f. = 9, $t = 0.261$, $P = 0.800$). At Calibishie, the interaction context:species effect on perch height

is explained by the significant difference between the two species in sympatry (contrast Tukey: d.f. = 359, $t = -2.415$, $P = 0.016$), while in allopatry, the two species used the same perch height (contrast Tukey: d.f. = 359, $t = 1.124$, $P = 0.262$). At Calibishie only, females perched lower than males for both species (Table 2).

At both island and Calibishie scales, neither species nor contexts differed in perch diameter, but at Calibishie, females used broader perches than males (Table 2).

BODY AND LIMB MORPHOLOGY

The first two varimax PCA axes explained a total variance of 42% (axis one RC1: 24%; axis two RC2:

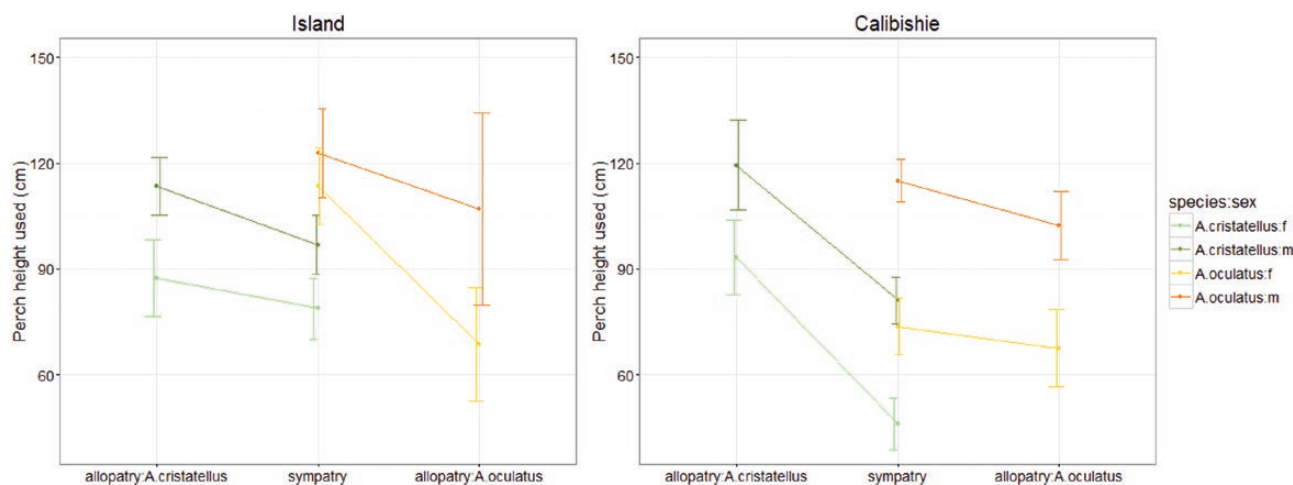


Figure 2. Perch height used (mean \pm SE) across species (green: *Anolis cristatellus*, orange: *Anolis oculatus*), context (allopatry and sympatry) and sex [females (f) and males (m)] at island (left) and Calibishie (right) scales.

Table 3. Relative contributions of the body and limb traits on each varimax PCA axis (RC1 and RC2), h2 (communalities), u2 (the uniquenesses) and com (the complexity of the factor loadings for that variable) for the two analyses at the island and Calibishie scales

Varimax	Island					Calibishie				
	Trait	RC1	RC2	h2	u2	com	RC1	RC2	h2	u2
Body mass	0.21	0.73	0.58	0.42	1.2	0.16	0.77	0.62	0.38	1.1
Body length	0.43	-0.38	0.33	0.67	2.0	-0.34	0.23	0.17	0.83	1.7
Body width	0.04	0.82	0.67	0.33	1.0	0.06	0.79	0.62	0.38	1.0
Body height	0.44	0.37	0.33	0.67	1.9	0.00	0.61	0.37	0.63	1.0
Femur	0.70	0.12	0.50	0.50	1.1	0.65	0.15	0.44	0.56	1.1
Tibia	0.80	0.18	0.67	0.33	1.1	0.73	0.43	0.72	0.28	1.6
Metatars	0.69	0.29	0.56	0.44	1.3	0.66	0.25	0.50	0.50	1.3
Longest hindlimb toe	0.52	0.01	0.28	0.72	1.0	0.52	0.41	0.44	0.56	1.9
Humerus	0.48	0.35	0.36	0.64	1.8	0.70	-0.09	0.49	0.51	1.0
Radius	0.30	0.39	0.24	0.76	1.9	0.58	0.05	0.33	0.67	1.0
Metacarpus	0.12	0.40	0.18	0.82	1.2	0.23	0.34	0.17	0.83	1.8
Longest forelimb toe	0.52	0.28	0.34	0.66	1.5	0.53	0.21	0.33	0.67	1.3

Bold values represent traits loading highly on each axis (over 0.6).

18%) at the island scale and 44% (RC1: 25%; RC2: 19%) at Calibishie scale. In both the island-wide and Calibishie analyses, the first PC axis (i.e. RC1) loads most strongly for limb traits, while the second PC axis (i.e. RC2) represents body stoutness (Table 3).

1. Limb axis

At the island-wide scale, the interaction between species and context factors is significant (d.f. = 202, $t = -2.355$, $P = 0.019$) due to significant differences between the two species in sympatry (contrast Tukey: d.f. = 202, $t = 6.659$, $P < 0.001$), but not in allopatry (contrast Tukey: d.f. = 202, $t = 0.260$, $P = 0.795$). This is explained by shorter limbs in *A. oculatus* and longer limbs in *A. cristatellus* in sympatry compared to allopatry (Fig. 3). Species and sex also interact significantly (d.f. = 202, $t = -5.160$, $P < 0.001$) due to significant sexual

dimorphism in limb traits in *A. cristatellus* (contrast Tukey: d.f. = 202, $t = -6.015$, $P < 0.001$), but not in *A. oculatus* (contrast Tukey: d.f. = 202, $t = 1.226$, $P = 0.221$). Males (contrast Tukey: d.f. = 202, $t = 5.221$, $P < 0.001$) but not females (contrast Tukey: d.f. = 202, $t = -0.151$, $P = 0.880$) of both species were also significantly different.

At Calibishie, females have shorter limbs than males for both species (d.f. = 335, $t = 7.708$, $P < 0.001$). *Anolis cristatellus* has longer limbs than *A. oculatus* (d.f. = 335, $t = -5.658$, $P < 0.001$; Table 4), and differences between contexts were not significant (Table 4).

2. Body axis

At the island-wide scale, while there is no significant effect of context nor sex on the body traits,

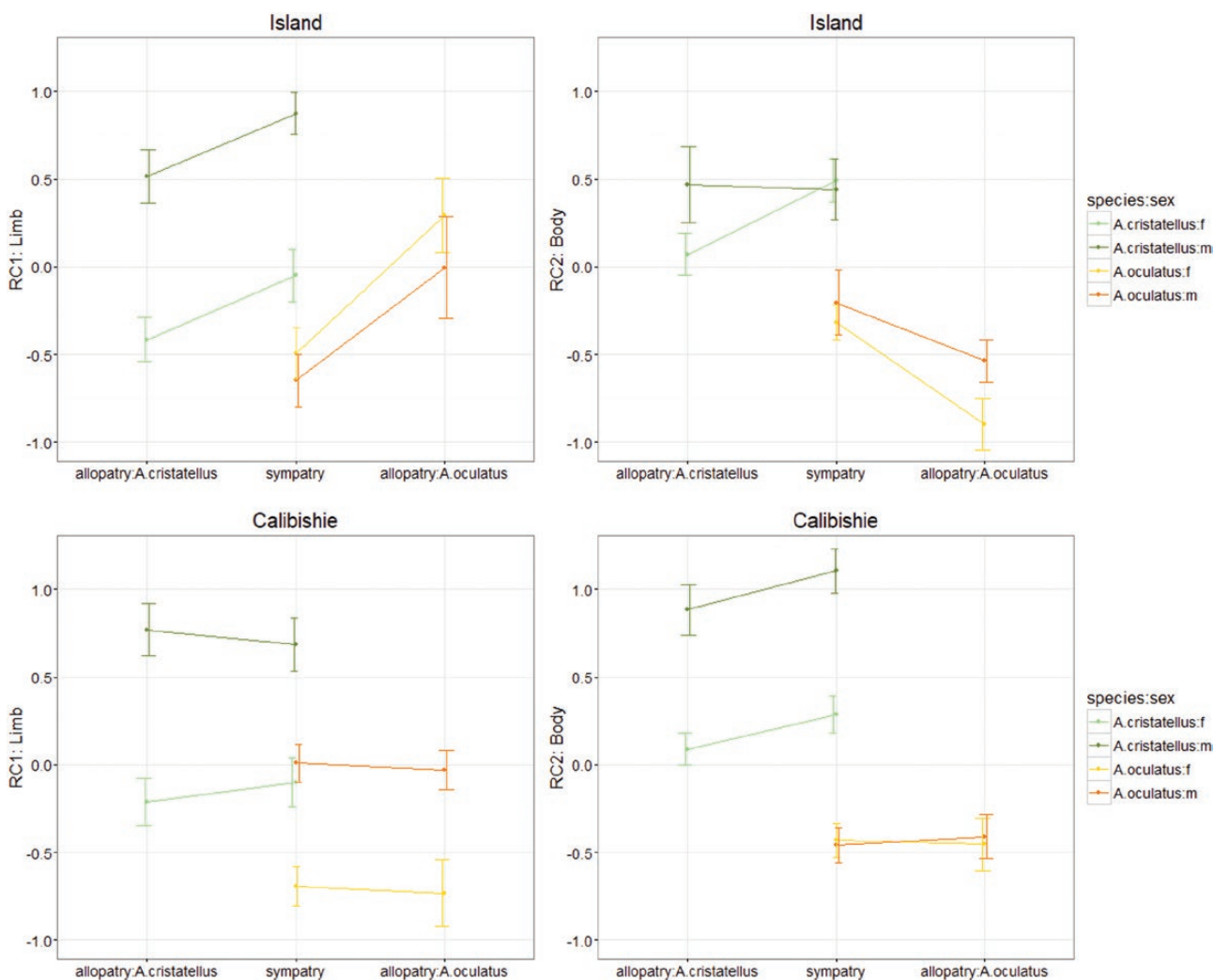


Figure 3. The first two varimax PCA axis values (RC1: limb and RC2: body; mean \pm SE) across species (green: *Anolis cristatellus*, orange: *Anolis oculatus*), sex [females (f) and males (m)] and context (allopatry and sympatry) at island (top) and Calibishie (bottom) scales.

A. cristatellus exhibits greater (i.e. more massive) body stoutness than *A. oculatus* (d.f. = 204, $t = -6.249$, $P < 0.001$; Table 4).

At the Calibishie scale, females are overall less stout than males (sex, d.f. = 334, $t = 5.908$, $P < 0.001$) and *A. cristatellus* is more stout than *A. oculatus* (species: d.f. = 334, $t = -4.265$, $P < 0.001$). However, a significant interaction between species and sex was observed (d.f. = 334, $t = -4.496$, $P < 0.001$). *Anolis cristatellus*, but not *A. oculatus*, showed a significant sexual dimorphism for body stoutness (*A. cristatellus* contrast Tukey: d.f. = 334, $t = -5.908$, $P < 0.001$; *A. oculatus* contrast Tukey: d.f. = 334, $t = 0.066$, $P = 0.948$).

TOEPAD MEASUREMENTS

At the island scale, the relative number of foot lamellae was lower for females than for males (sex: d.f. = 200, $t = 3.731$, $P < 0.001$) and for *A. cristatellus* compared to *A. oculatus* (d.f. = 200, $t = 3.953$, $P < 0.001$). However, the three-way interaction between context, species and sex is also significant (context:species:sex d.f. = 200, $t = -2.297$, $P = 0.023$). To disentangle the effect of each factor, we performed separate analyses (Supporting Information, Table S1) showing that the divergence between the two species in sympatry is due to the decrease of foot lamella number for female *A. cristatellus* in contrast to the increase of foot lamellae number in female *A. oculatus* (Supporting Information, Table S1; Table 5; Fig. 4).

At both scales, neither foot and hand toepad area nor hand toepad lamellae number differs between contexts. Females possess smaller hand and foot toepad areas as well as hand lamellae number compared

to males (Table 5). Also, the foot and hand toepad areas do not differ between the species for females, but are higher for male *A. cristatellus* than *A. oculatus* (Supporting Information, Table S2). The pattern is different for the hand lamella number where both male and female *A. oculatus* present higher values compared to *A. cristatellus*. At Calibishie, *A. oculatus* presents higher foot lamella number than *A. cristatellus* (Supporting Information, Table S2).

DISCUSSION

This study reveals rapid ecological character displacement resulting from the invasion of an ecologically similar species to an island containing only one native species of *Anolis* lizard. In sympatric populations, the native *A. oculatus* used higher perches, while the invasive *A. cristatellus* used lower perches compared to allopatric populations of both species (Fig. 5). This habitat shift is associated with a change in limbs and toepads in populations that have been sympatric with the invader for a decade or more (Fig. 5). However, in populations in which sympatry has only recently occurred (within the past 2 years, in the Calibishie region), the same perch height shifts were observed without concomitant morphological change. Our prediction is that continued sympatry in Calibishie will lead to a morphological change in the near future, just as it has elsewhere in the island.

The habitat use and morphological (limb and toepad) divergences observed between *A. cristatellus* and *A. oculatus* in sympatry are in accordance with the results of *Anolis* invasions elsewhere. For example, Stuart *et al.* (2014) recorded the native *A. carolinensis*

Table 4. Statistical results from the final linear mixed-effect models (based on AIC) testing the two varimax PCA axes (RC1 and RC2) according to the variables (i.e. species, context, sex and all the interactions) at the island-wide and Calibishie scales

	Variable	Island					Calibishie				
		Value	SE	d.f.	<i>t</i> -value	<i>P</i> -value	Value	SE	d.f.	<i>t</i> -value	<i>P</i> -value
RC1: limb	Intercept	-0.406	0.234	202	-1.738	0.084	-0.124	0.136	335	-0.917	0.360
	Context	0.344	0.272	9	1.265	0.238	0.027	0.144	7	0.184	0.859
	Species	0.478	0.367	202	1.303	0.194	-0.646	0.114	335	-5.658	< 0.001
	Sex	0.948	0.158	202	6.015	< 0.001	0.774	0.100	335	7.708	< 0.001
	Context:species	-0.888	0.377	202	-2.355	0.019	NA	NA	NA	NA	NA
	Species: sex	-1.137	0.220	202	-5.160	< 0.001	NA	NA	NA	NA	NA
RC2: body	Intercept	0.191	0.259	204	0.738	0.461	0.167	0.145	334	1.154	0.249
	Context	0.149	0.328	9	0.454	0.661	0.065	0.150	7	0.432	0.679
	Species	-0.889	0.142	204	-6.249	< 0.001	-0.673	0.158	334	-4.265	< 0.001
	Sex	0.210	0.112	204	1.874	0.062	0.812	0.137	334	5.908	< 0.001
	Species:sex	NA	NA	NA	NA	NA	-0.819	0.182	334	-4.496	< 0.001

The significant results are in bold. AIC, Akaike information criterion; NA, not applicable; PCA, principal component analysis.

Table 5. Statistical results from the final linear mixed-effect models (based on AIC) testing the toepad traits according to the variables (i.e. species, context, sex and all the interactions) at the island-wide and Calibishie scales

Trait	Variable	Island				Calibishie							
		Value	SE	d.f.	t-value	P-value	Value	SE	d.f.	t-value	P-value		
Toepad	Foot toepad area												
	Intercept	-7.187	0.384	203	-18.722	0.000	-7.026	0.292	339	-24.079	0.000		
	Context	-0.061	0.036	9	-1.699	0.124	-0.010	0.011	7	-0.959	0.369		
	Species	0.004	0.034	203	0.109	0.913	-0.043	0.026	339	-1.675	0.095		
	Sex	0.220	0.044	203	4.975	<0.001	0.263	0.032	339	8.106	<0.001		
	Log(SVL)	2.131	0.102	203	20.867	0.000	2.084	0.078	339	26.813	0.000		
	Species:sex	-0.142	0.033	203	-4.318	<0.001	-0.125	0.024	339	-5.115	<0.001		
	Intercept	2.304	0.164	200	14.024	0.000	2.707	0.166	346	16.303	0.000		
	Context	-0.019	0.018	9	-1.101	0.299	0.003	0.008	7	0.417	0.689		
	Species	0.082	0.021	200	3.953	<0.001	0.192	0.015	346	13.034	<0.001		
Foot lamellae number	Sex	0.085	0.023	200	3.731	<0.001	0.172	0.018	346	9.365	<0.001		
	Log(SVL)	0.166	0.043	200	3.815	0.000	0.044	0.044	346	1.000	0.318		
	Context:species	0.052	0.024	200	2.135	0.034	NA	NA	NA	NA	NA		
	Species:sex	0.021	0.027	200	0.769	0.443	-0.066	0.014	346	-4.861	0.000		
	Context:sex	0.044	0.022	200	1.940	0.054	NA	NA	NA	NA	NA		
	Context:species:sex	-0.076	0.033	200	-2.297	0.023	NA	NA	NA	NA	NA		
	Intercept	-8.439	0.448	205	-18.826	0.000	-9.285	0.375	346	-24.780	0.000		
	Context	-0.018	0.040	9	-0.451	0.663	0.007	0.027	7	0.258	0.804		
	Species	0.066	0.040	205	1.647	0.101	0.061	0.034	346	1.813	0.071		
	Sex	0.321	0.051	205	6.257	<0.001	0.304	0.041	346	7.402	<0.001		
Hand toepad area	Log(SVL)	2.215	0.119	205	18.578	0.000	2.427	0.100	346	24.367	0.000		
	Species:sex	-0.169	0.038	205	-4.408	<0.001	-0.189	0.030	346	-6.239	<0.001		
	Intercept	1.257	0.211	205	5.961	0.000	1.332	0.236	351	5.650	0.000		
	Context	0.011	0.014	9	0.731	0.483	0.004	0.019	7	0.232	0.823		
	Species	0.190	0.019	205	10.014	<0.001	0.291	0.021	351	13.655	<0.001		
	Sex	0.208	0.024	205	8.489	<0.001	0.233	0.026	351	9.012	<0.001		
	Log(SVL)	0.257	0.056	205	4.592	0.000	0.227	0.063	351	3.621	0.000		
	Species:sex	-0.082	0.019	205	-4.316	<0.001	-0.092	0.019	351	-4.848	<0.001		

The significant results are in bold. AIC, Akaike information criterion; NA, not applicable.

in Florida perching higher in the presence of the invasive *A. sagrei*; a similar shift was exhibited by *Anolis conspersus* on Grand Cayman in the presence of invasive *A. sagrei* (Losos, Marks & Schoener, 1993). More generally, a large body of observational and experimental comparative data indicate that anoles alter their habitat use in the presence of sympatric congeners to minimize overlap (e.g. Schoener, 1975; Lister, 1976a; Pacala & Roughgarden, 1985; reviewed in Losos, 2009). Also, similar to the situation in Dominica, data both from invasive species and from comparisons of natural populations indicate that species diverge in morphology according to the new habitat used (e.g. toepad reviewed in Stuart *et al.*, 2014; limb length reviewed in Losos, 2009) when sympatric with other anoles (see also Schoener, 1970; Lister, 1976b).

The morphological shifts observed in Dominica are in accordance with adaptive morphological differences seen among other anole species (reviewed in Losos, 2009). In general, more terrestrial species tend to have longer legs, better for running rapidly on broad surfaces, whereas species using higher perches evolve shorter legs for stability. In addition, better-developed toepads occur in more arboreal species, providing greater clinging capability. The shifts observed in the island-scale comparisons between *A. cristatellus*, which becomes more terrestrial in sympatry, and *A. oculatus*, which becomes more arboreal, are consistent with these trends. One anomaly with our results, however, is that we did not find *A. oculatus* in sympatry to be using narrower perches. Among anole species, those that perch higher tend to use narrow perches and thus evolve shorter limbs for agility. It is

possible that shorter limbs in *A. oculatus* are evolving for other reasons. Alternatively, it is certainly true that lizards using more arboreal habitats encounter more narrow branches than those on the tree trunk near the ground, so selection may have been favouring shorter limbs in these populations, even if we failed to observe the lizards using narrower branches. It may be that the sympatric *A. oculatus* do use narrow branches higher in the tree, but do so only rarely and thus were not observed.

The island-scale differences on the limb and toe-pad traits between sympatric and allopatric populations could be explained either as evolved genetic differences or as the result of phenotypic plasticity. The fact that the ecological differences also occur at Calibishie, but are not accompanied by morphological changes, suggests that phenotypic plasticity is not involved. Rather, it suggests that the differences observed at the island scale are genetically based. The Calibishie populations, which have only been in sympatry for 2 years, have not yet had time to evolve adaptively in response to the new conditions (alternatively, the short distance between study sites in Calibishie may lead to high levels of gene flow, preventing evolutionary divergence). Nonetheless, the plasticity hypothesis should be tested directly in both species with a common garden study. Such a study was conducted on *A. oculatus* from different populations occurring across a rainfall and temperature gradient environment across Dominica. This study found minimal evidence for phenotypic plasticity, suggesting that the inter-population differences were genetically based (Thorpe, Reardon & Malhotra, 2005).

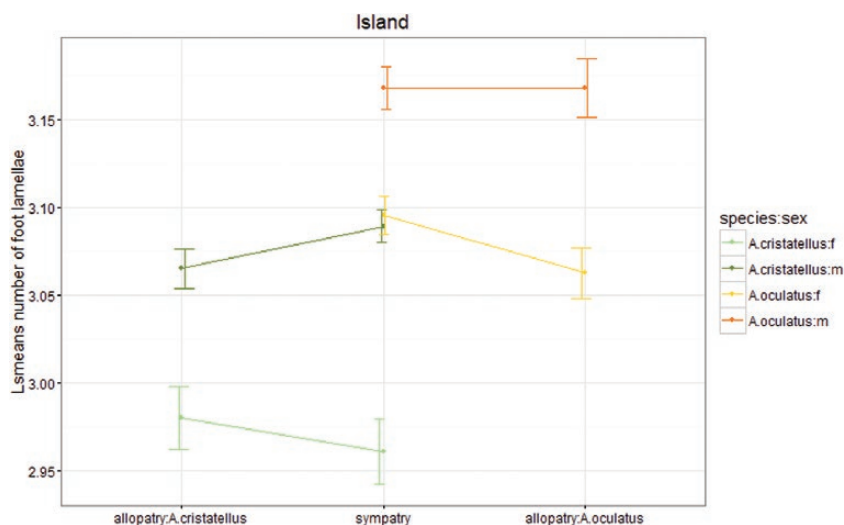


Figure 4. Lsmeans from the linear mixed-effect models testing for the number of foot lamellae (mean \pm SE) according to the context (allopatry vs. sympatry), the species (green: *Anolis cristatellus* and orange: *Anolis oculatus*) and the sex [females (f) and males (m)] at the island-wide scale. The least squares means are the predicted marginal means that summarized linear model that includes factors.

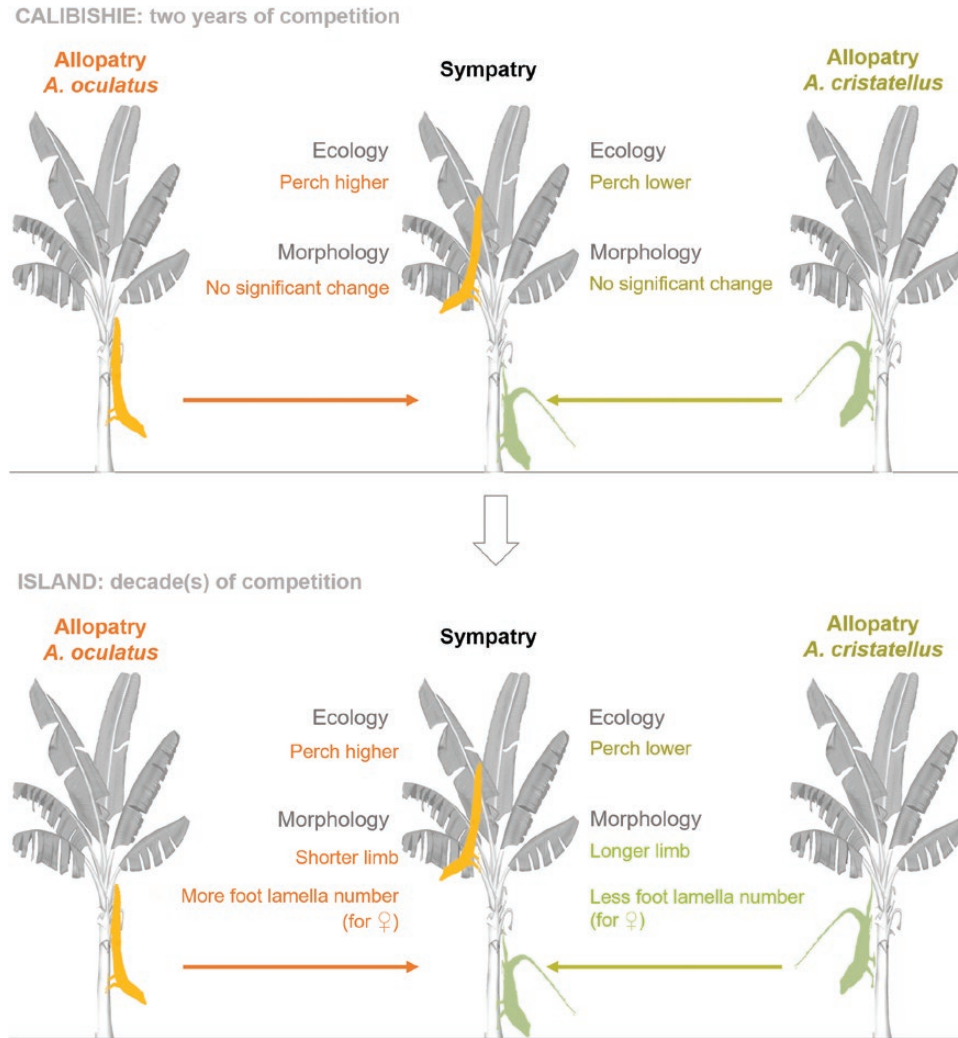


Figure 5. Summary of the main results shown in this study at Calibishie (top) and island (bottom) scales. For each scale, the main ecological and morphological changes from allopatry to sympatry are shown for *Anolis oculatus* (in orange) and *Anolis cristatellus* (in green), for males and females unless stated.

Our study also finds evidence for sex-specific selective pressures differing between allopatry and sympatry. Why such divergence between sexes occurred is not clear. However, sexual dimorphism is widespread in anoles (Butler, Schoener & Losos, 2000; Butler, 2007; Butler, Sawyer & Losos, 2007), and at least, size dimorphism changes as a function of the number of congeneric anole species (Schoener, 1969). In particular, our study revealed that only females diverged in the number of foot lamellae in sympatry, emphasizing the fact that males and females may respond differently to the same perch height shift due to interspecific competition. Indeed, the interaction between traits may differ between the sexes, as it was shown in *Anolis carolinensis* for which the females – using broader perches – exhibited longer hindlimbs relative to SVL, while this relationship was exclusively allometric for males (Dill *et al.*, 2013).

Contrary to the limb and toepad morphological traits, body stoutness did not change between allopatric and sympatric populations in either Calibishie or island-wide scales. This result may suggest that, even if the competition between the two species occurs, it may not drive a reduction in body condition for either species. Nevertheless, the nature of the competitive selection between *A. cristatellus* and *A. oculatus* is still unknown, as the interspecific competition may be by exploitation (e.g. for limited food resources) or by interference (e.g. direct agonistic encounter; Grether *et al.*, 2009). Regardless of the type of interaction driving the habitat shift, our results challenge previous suggestions (Malhotra *et al.*, 2007; Daniells *et al.*, 2008) that the native *A. oculatus* is unlikely to be able to coexist with the invasive *A. cristatellus* competitor. In contrast, *A. oculatus* is the larger of the two species, and

when we observed interspecific agonistic encounters, it was the aggressor, rather than *A. cristatellus* (C. Dufour, pers. observ.). Nonetheless, other mechanisms such as better parasite resistance may play a role in the coexistence of the two species (Schall, 1992).

Over a relatively short period (less than two decades), *A. cristatellus* has spread throughout much of lowland Dominica. Future monitoring will be important to track the spread of this invasive species and record its impact. Although we argue previously that *A. oculatus* is able to coexist with the invader, future study is necessary to analyse whether patterns change through time. Certainly, by comparison to the substantial ecological and morphological divergence seen in the evolutionary radiation of Caribbean anoles (Losos, 2009), we might expect divergence in ecology and morphology to increase considerably in the future. Moreover, Dominica is a rugged, mountainous island, and to date, *A. cristatellus* is only found in the lowlands. It would be reasonable to predict that *A. cristatellus* may adapt to cooler, more montane conditions and thus expand its range altitudinally. Should it do so, it will be interesting to observe whether patterns of sympatric divergence differ at different altitudes.

SHARED DATA

Data deposited at Dryad. doi:10.5061/dryad.8mr63.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Foot and hand toepad pictures of a male *Anolis oculatus* showing (A) 24 and (B) 15 lamellae on the fourth toe, which is the longest. The toepad area was measured between the two lamellae indicated by the red arrows.

Table S1. Statistical results from the final linear mixed-effect models (based on AIC) testing the foot toepad lamellae number by separating the two sexes, contexts and species according to species and/or context and/or sex (depending on the analysis) and the two-way interactions at the island-wide scale.

Table S2. Post hoc tests for the foot and hand toepad area and hand lamella number at both scales and for foot lamellae number at Calibishie scale. For each sex, the species effect was tested with contrast Tukey post hoc tests.