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Observing character displacement from process to pattern in a novel vertebrate community

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James T. Stroud [1] ✉, **Sean T. Giery** [2], **Robert J. P. Heathcote** [3], **Sarin Tiatragul** [4], **Michael L. Yuan** [5], **Kenneth J. Feeley** [6] & **Jonathan B. Losos** [7]

Ecological character displacement, whereby shifts in resource use in the presence of competing species leads to adaptive evolutionary divergence, is widely considered an important process in community assembly and adaptive radiation. However, most evidence for character displacement has been inferred from macro-scale geographic or phylogenetic patterns; direct tests of the underlying hypothesis of divergent natural selection driving character displacement in the wild are rare. Here, we document character displacement between two ecologically similar lizards (*Anolis sagrei* and *A. cristatellus*) experiencing novel contact. We identify directional selection during the incipient stages of sympatry in a new community that corresponds to repeated trait divergence across multiple established sympatric communities. By identifying the role of natural selection as character displacement unfolds, we connect how natural selection operating at short timescales may drive broader patterns of trait distributions at larger spatial and temporal scales.

Ecologically similar species typically differ in resource use and morphology when co-occurring. Character displacement, the process by which adaptive divergence by natural selection drives such ecomorphological patterns, has long been assumed responsible for many such scenarios[1–5]. Evidence for character displacement has classically been drawn from broadscale patterns of geographic or phylogenetic trait distributions, whereby closely related species or those that co-occur in space differ in resource-acquiring traits[1,6–8]. However, although robust statistical patterns are often detected that fit with the expectations of character displacement[9–13]—and mechanisms proposed to explain them[14], the nature of these macro-scale comparative data typically precludes direct examination of underlying processes[4,6,8,15]. As such, there remains confusion about the underlying processes that drive character displacement in the wild[16].

A major barrier to studying the processes that drive character displacement is that opportunities to observe novel contact between similar species in nature are limited. Here, our research on introduced non-native Caribbean *Anolis* lizards (anoles) in south Florida, USA, provides a rare exception. The independent introduction of two ecomorphologically convergent lizards to south Florida—the Cuban brown anole (*Anolis sagrei*; Fig. 1A) and the Puerto Rican crested anole (*A. cristatellus*)—set the stage for character displacement to ensue[17,18]. As these species originate from separate Caribbean island radiations[19], contact in Florida represents their first interactions, providing an unparalleled opportunity to test the character displacement hypothesis in the wild.

Previous research had suggested character displacement might be occurring between *A. sagrei* and *A. cristatellus* in Miami, south Florida, via divergence in perch height[17]. However, this research was limited to a single location where sympatry had only been established for approximately five years[17], preventing the investigation of longer-term evolutionary responses. To expand on this preliminary finding, we selected nine sites across Miami (three allopatric sites per species and three sympatric sites that include both species; Supplementary

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[1]School of Biological Sciences, Georgia Institute of Technology, Atlanta, GA, USA. [2]Department of Biological Sciences, Ohio University, Athens, OH, USA. [3]Department of Biology, University of Oxford, Oxford, UK. [4]Division of Ecology & Evolution, Research School of Biology, The Australian National University, Canberra, ACT, Australia. [5]Center for Population Biology, University of California, Davis, CA, USA. [6]Department of Biology, University of Miami, Coral Gables, FL, USA. [7]Department of Biology, Washington University in St. Louis, St. Louis, MO, USA. ✉e-mail: stroud@gatech.edu

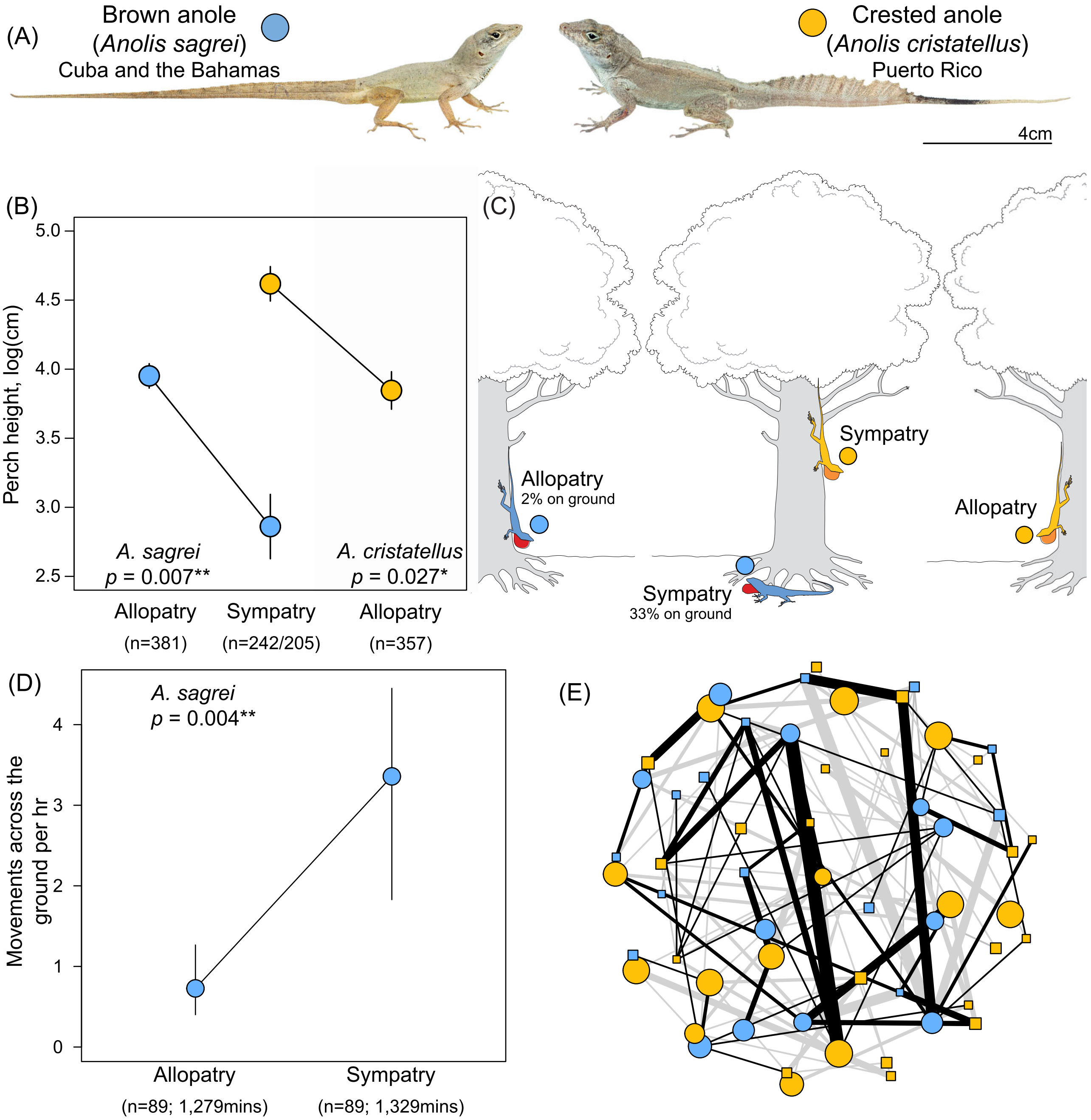

Fig. 1 | Comparative evidence for character displacement via shifts in behavior and habitat use. A *Anolis sagrei* and *A. cristatellus*. **B** When in allopatry, both species occupy similar perch heights but diverge when in sympatry. Circles represent mean values from three sites per treatment; error bars are ± 1 S.E. **C** Lower perch height in sympatric *A. sagrei* populations is primarily driven by increased terrestriality (values represent mean percentage of lizards observed on the ground across three sites in each treatment). **D** Sympatric *A. sagrei* moved across the ground between plant perching sites at a significantly higher frequency relative to those in allopatry. Circles represent mean values; error bars are ± 1 S.E. *P*-values in (**B**) and (**D**) are from linear mixed effects models with treatment (i.e., allopatry vs. sympatry) as a fixed effect and site as a random effect. $^*p < 0.05$; $^{**}p < 0.01$. **E** A mixed species social network in a sympatric community (MHS) estimated from association by distance measurements. Each symbol (node) represents an individual lizard (squares = males; circles= females), and size is proportional to body size. Black lines (edges) represent the presence of inter-specific interactions between individual *A. sagrei* and *A. cristatellus* lizards; light gray edges show intra-specific interactions. Edge thickness demonstrates the strength of the interaction relationship between two individual lizards. Photo credit: Day's Edge Prods. All source data are available at: https://doi.org/10.6084/m9.figshare.27165759; data for (**B**, **C**) from file "NatComms_ECD_perch data"; data for (**D**) from file "NatComms_ECD_movement behaviors"; data for (**E**) from files "NatComms_ECD_sympatric network_attributes" and "NatComms_ECD_sympatric network_groups.csv".

Tables 1 and 2and Supplementary Fig. 1), where species had been established for over 30 generations[17,20,21], to explore the geographic consistency of character displacement. We predicted that divergence in habitat use would occur in all sympatric sites as previously recorded[17]; *A. sagrei* perches lower and exhibits increased terrestriality in sympatry, whereas *A. cristatellus* perches higher.

As the form-function relationship associated with habitat use is well resolved in anoles[19], clear predictions can be made about how shifts in habitat use may lead to changes in morphology. In the context of perch height divergence, more terrestrial anole species typically have relatively longer limbs than arboreal species[22,23] as longer limbs facilitate faster maximal sprint speed on broad surfaces[24,25] such as the

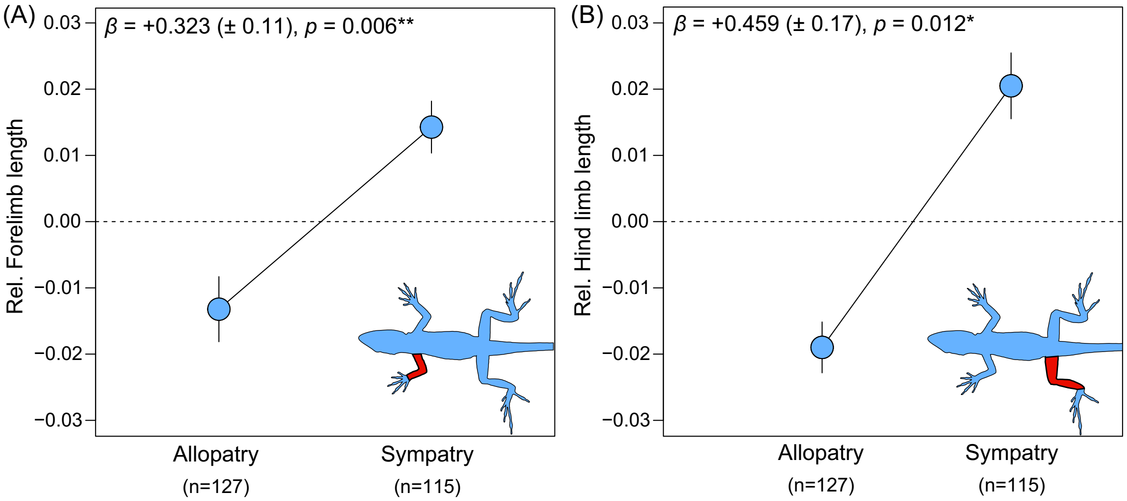

Fig. 2 | Comparative evidence for character displacement via shifts in key morphological traits associated with habitat use. Sympatric *A. sagrei* had relatively longer (**A**) forelimbs, and (**B**) hind limbs compared to allopatric populations. Blue circles represent mean trait values from three sites per treatment; error bars represent 95% C.I. *P*-values are from linear mixed effects models with treatment (i.e., allopatry vs. sympatry) as a fixed effect and site as a random effect. $^{*}p < 0.05$; $^{**}p < 0.01$. All source data are available at: https://doi.org/10.6084/m9.figshare.27165759; data for (**A**, **B**) from file "NatComms_ECD_morphology".

ground. If we observe that sympatric *A. sagrei* populations are more terrestrial than allopatric populations, then we would predict that *A. sagrei* would exhibit relatively longer limbs in sympatry.

As a result of an ongoing but independent study[26], we had the serendipitous chance to test the hypothesis that shifts in natural selection occur during the incipient stages of character displacement. After studying natural selection for two years in an *Anolis* community that included *A. sagrei* (2016–2017, ref. 26), *A. cristatellus* invaded. Our analysis of selection prior to the arrival of *A. cristatellus* presented a unique opportunity to explore if changes in selection pressure occur when *A. sagrei* and *A. cristatellus* first come into contact and subsequently lead to divergent adaptive evolution. If *A. sagrei* limb length differs as expected between established sympatric and allopatric *A. sagrei* populations in our geographic comparative analysis, then we predicted that we would see directional selection favoring relatively longer limbs following the invasion of *A. cristatellus*.

Here, we first use a comparative approach to explore the geographic consistency of character displacement among established sympatric and allopatric populations in Florida. To do this, we explore differences in habitat use, movement behavior, and associated key morphological traits. Second, the formation of a new sympatric community on the expanding invasion front of *A. cristatellus* presented us with the opportunity to observe the incipient stages of character displacement in real-time. Informed by our geographic patterns of character displacement, we then test for shifts in natural selection in this *A. sagrei* population before and after the invasion of *A. cristatellus*.

Results

Identifying an established pattern of character displacement

In allopatry, *A. sagrei* and *A. cristatellus* did not differ in habitat use (i.e., perch height, Fig. 1B; Linear Mixed Model: $\beta = 0.19$, $t_{5,741} = 0.282$, $p = 0.793$; Supplementary Table 3). Conversely, in sympatry, *A. sagrei* and *A. cristatellus* differed in perch height (Fig. 1B; $\beta = -5.02$, $t_{2,461} = -7.49$, $p = 0.004$); *A. cristatellus* perches higher ($\beta = 3.22$, $t_{5,563} = 3.49$, $p = 0.027$) and *A. sagrei* perches lower than those in allopatry ($\beta = -1.98$, $t_{5,639} = -5.89$ $p = 0.007$). Specifically, we observed significantly more *A. sagrei* on the ground in sympatric versus allopatric populations (33.4% [±18.5] vs. 1.6% [±1.5], respectively; $\chi^2 = 29.7$, $p < 0.001$). Sympatric and allopatric *A. sagrei* were very similar in most movement behaviors (Supplementary Table 5), except that sympatric *A. sagrei* moved across the ground over four-and-a-half times more frequently than when in allopatry (Fig. 1D; Linear Mixed Model: 0.73 vs. 3.36 movements per hour; $\beta = 0.48$, $t_{5,178} = 2.91$, $p = 0.004$). Despite perch height divergence in sympatry (Fig. 1B), interspecific interactions were common (Fig. 1E; black edges). Interspecific diet overlap was high in both allopatry (prey diversity, Schoener's $D = 0.89$; prey size, $\beta = -0.69$, $F_{5,304} = 1.59$, $p = 0.283$) and sympatry (prey diversity, Schoener's $D = 0.75$; prey size, $\beta = -0.18$, $F_{5,262} = 0.49$, $p = 0.483$).

Anolis sagrei body size did not differ between sympatric and allopatric sites (Linear Mixed Model: $\beta = 0.63$, $t_{5,235} = 2.46$, $p = 0.079$). However, while accounting for body size, lizards in sympatric populations had relatively longer hind limbs (Fig. 2; $\beta = 0.46$, $t_{5,235} = 2.70$, $p = 0.012$) and forelimbs ($\beta = 0.32$, $t_{4,235} = 3.03$, $p = 0.006$) than those in allopatric populations. We observed no difference in *A. cristatellus* body size ($\beta = -0.44$, $t_{5,211} = -2.14$, $p = 0.108$), relative forelimb length ($\beta = 0.28$, $t_{5,211} = 1.70$, $p = 0.069$) or relative hind limb length ($\beta = 0.16$, $t_{5,211} = 0.78$, $p = 0.358$) between sympatric and allopatric populations (Supplementary Table 6).

We found minimal evidence of population structure in *A. sagrei* across sampling sites. Admixture analyses (*NGSadmix*, ref. 27) indicated a best-fit model of $K = 3$, although ΔK does not allow for assessment of $K = 1$ models[28], with genetic demes that do not correspond to allopatric versus sympatric sites (Supplementary Fig. 2). Furthermore, F_{ST} between allopatric and sympatric sites was low ($F_{ST} = 0.015$). We also found no signal of genetic isolation-by-distance based on identity-by-state (Mantel $r = 0.052$, $p = 0.192$).

Observing the incipient stages of character displacement

Due to the presence of *A. cristatellus* and subsequent ecological predictions of increased resource competition, we predicted *A. sagrei* would decrease in both population size and relative abundance in this community. Prior to *A. cristatellus* presence, *A. sagrei* represented 72–85% of all individual adult anoles in this community. The adult male *A. sagrei* population ranged from 108 (May 2016) to 168 (October 2017) individuals. After *A. cristatellus* invaded in late 2017, the population size and relative abundance of *A. sagrei* began to decline. Within four years, *A. sagrei* decreased from representing 75% of all adult anoles in the community (October 2017) to just 18% (October 2021), by which time *A. cristatellus* represented 66% of all adult anoles. The population size of adult male *A. sagrei* fell from 168 individuals (October 2017) to 54 individuals (October 2021). In the established sympatric communities from our earlier comparative analysis, the relative abundance of each species varied from 33–72% (*A. sagrei*) and 22–56% (*A. cristatellus*) of all individual, adult anoles.

From our comparative analyses, we developed three hypotheses to test using our selection data. First, we hypothesized that the invasion of *A. cristatellus* would lead to changes in selection pressures on the limb lengths of *A. sagrei*. We detected significant shifts in selection on both forelimbs ($\chi^2 = 4.43$, $p = 0.035$) and hind limbs ($\chi^2 = 5.37$, $p = 0.020$). Second, we hypothesized that changes in selection would favor relatively longer limbs. We observed that selection on relative forelimb length of *A. sagrei* changed from weak negative directional selection to stabilizing selection (Table 1and Fig. 3A), with a corresponding shift in the fitness optima from relatively smaller to relatively longer forelimbs (Table 2and Fig. 3. A, B). For hind limbs, we observed no selection prior to the arrival of *A. cristatellus* (Fig. 3C), but subsequently detected strong positive directional selection favoring relatively longer hind limbs (Table 1and Fig. 3D). The fitness optimum shifted from relatively smaller to relatively longer hind limbs (Table 2and Fig. 3C, D). Lastly, we hypothesized that there would be correlated selection between forelimb and hind limb length: we detected strong correlational selection between forelimb and hind limb length after invasion that was not present prior (Table 1and Fig. 3E, F).

After observing changes in selection on limb length immediately after the invasion of *A. cristatellus* (Table 1), we predicted that the population would exhibit relatively longer limbs in subsequent generations. However, when resampled in 2022, approximately four to five generations after the invasion of *A. cristatellus*, the *A. sagrei* population did not exhibit relatively longer forelimbs ($F_{1,419} = 0.287$, $p = 0.592$) or hind limbs ($F_{1,419} = 0.064$, $p = 0.800$) than recorded in 2017.

As we observed no evolutionary change in hind limb length despite the detection of strong directional selection (Fig. 3D), we next employed the Breeder's equation[29] using our observed selection differentials (*s*) and published heritability values for *A. sagrei* hind limb lengths[30] to estimate the number of generations that it would take to observe a change in hind limb length corresponding to the proportional differences between *A. sagrei* in our sympatric versus allopatric communities. We estimate that comparable increases in hind limb length would be expected to occur after ~14.4–18.6 generations. The sympatric populations in our comparative analysis have likely been established for 35–50 years[17,21,31,32], long enough for the differences in limb length that we observed to have evolved in situ.

Discussion

As the initiation of sympatry between ecologically similar species is rarely observed in nature, the study of character displacement has largely been retrospective, making inferences about the role of unobserved historic processes from present-day patterns of trait values. Integrative field studies that bridge this process-pattern divide, combining comparative approaches with field studies of underlying mechanisms, are scarce. Here, we document character displacement as both a process and a pattern during novel contact between two convergent Caribbean *Anolis* lizards independently introduced to South Florida, USA.

Our comparative analyses showing divergence in habitat use and associated morphological traits in established sympatric *A. sagrei* and *A. cristatellus* populations suggest that character displacement has occurred (Figs. 1, 2). Our molecular data show that allopatric and sympatric *A. sagrei* populations do not cluster into two groups, which suggests that the ecomorphological changes we observed in our sympatric communities occurred independently (Supplementary Fig. 2). However, these data preclude investigation of the underlying processes that led to this pattern. The formation of a new sympatric community via the invasion of *A. cristatellus* into an established *A. sagrei* allopatric population allowed us to study the incipient stages of character displacement in real-time. Prior to the invasion of *A. cristatellus*, we had been conducting a long-term study of natural selection in this *A. sagrei* population[26], allowing us to directly test for shifts in natural selection on key traits that our geographic analyses had suggested diverged during character displacement. In accordance with these comparative morphological data (Fig. 2), we detected strong directional selection in *A. sagrei* favoring individuals with relatively longer hind limbs after the invasion of *A. cristatellus* (Fig. 3). Taken together, our results provide direct evidence for the role of natural selection in driving character displacement in the wild.

Table 1 | Natural selection during the incipient stages of character displacement

Trait	β / γ	SE	z	p	
Pre-invasion ($n = 338$)					
Body size (SVL)	+0.663	0.472	+1.211	0.226	–
Forelimb length	−0.826	0.446	−1.800	0.072	–
Hind limb length	+0.174	0.496	+0.385	0.700	–
Forelimb x Hind limb	+0.114	0.231	+0.317	0.801	–
Post-invasion ($n = 569$)					
Body size (SVL)	−0.343	0.293	−1.391	0.164	–
Forelimb length	−0.265	0.255	−0.970	0.332	–
Forelimb length^2	−0.853	0.450	−2.051	0.040	*
Hind limb length	+0.878	0.296	+2.956	0.003	**
Forelimb x Hind limb	+0.817	0.476	+1.906	0.057	–

Mixed-effects models describing the relationship between key morphological traits and *Anolis sagrei* survival before and after the invasion of *A. cristatellus*. Both linear (β) and non-linear (quadratic and correlational, γ) selection coefficients are shown. All *p*-values are from multivariate selection models following Lande & Arnold[89]. *$p < 0.05$, **$p < 0.01$.

Given the detection of such strong directional selection on hind limb length, it was surprising to not observe the subsequent evolution of longer hind limbs in this *A. sagrei* population when re-measured after approximately four to five generations (June 2022). We suspect that too few generations have passed to observe the magnitude of hind limb divergence in this focal population as we recorded in our comparative populations (i.e., Fig. 2). Given the observed strength of directional selection on hind limb length (Table 1), limb length differences similar to those recorded between our sympatric and allopatric populations would be expected to occur after 14.4–18.6 generations. The sympatric populations in our comparative analysis have likely been established for 35–50 generations[17,21,31], suggesting our observed differences in hind limb lengths could have resulted from evolution by natural selection. Such evolutionary lag times can occur in natural populations, for example, due to weak trait heritability[33], developmental plasticity[34,35] (which could also, conversely, accelerate adaptive evolutionary responses[36,37]), or if the strength of selection varies through time, even if the direction remains constant[38]. For example, elsewhere in Florida, morphological evolution of the native green anole (*A. carolinensis*) in response to increased arboreality in the presence of invading *A. sagrei* was apparent after approximately 20 generations[39], providing comparative temporal support for the evolutionary dynamics that we predict are occurring in our study.

Our observed differences in limb length between established sympatric and allopatric communities (Fig. 2) could also have been the result of processes other than adaptive evolution by natural selection. For example, previous studies of laboratory populations of *Anolis* lizards have observed phenotypic plasticity in hind limb length[34,40,41]. As all prior evidence for limb length plasticity of *Anolis* lizards is derived from captive populations with access to only a limited range of structure habitat types (e.g., treatments with either only 'narrow' or 'wide' perches; refs. 40,41), it is unclear if wild populations also demonstrate such plasticity. Future tests of the plasticity versus

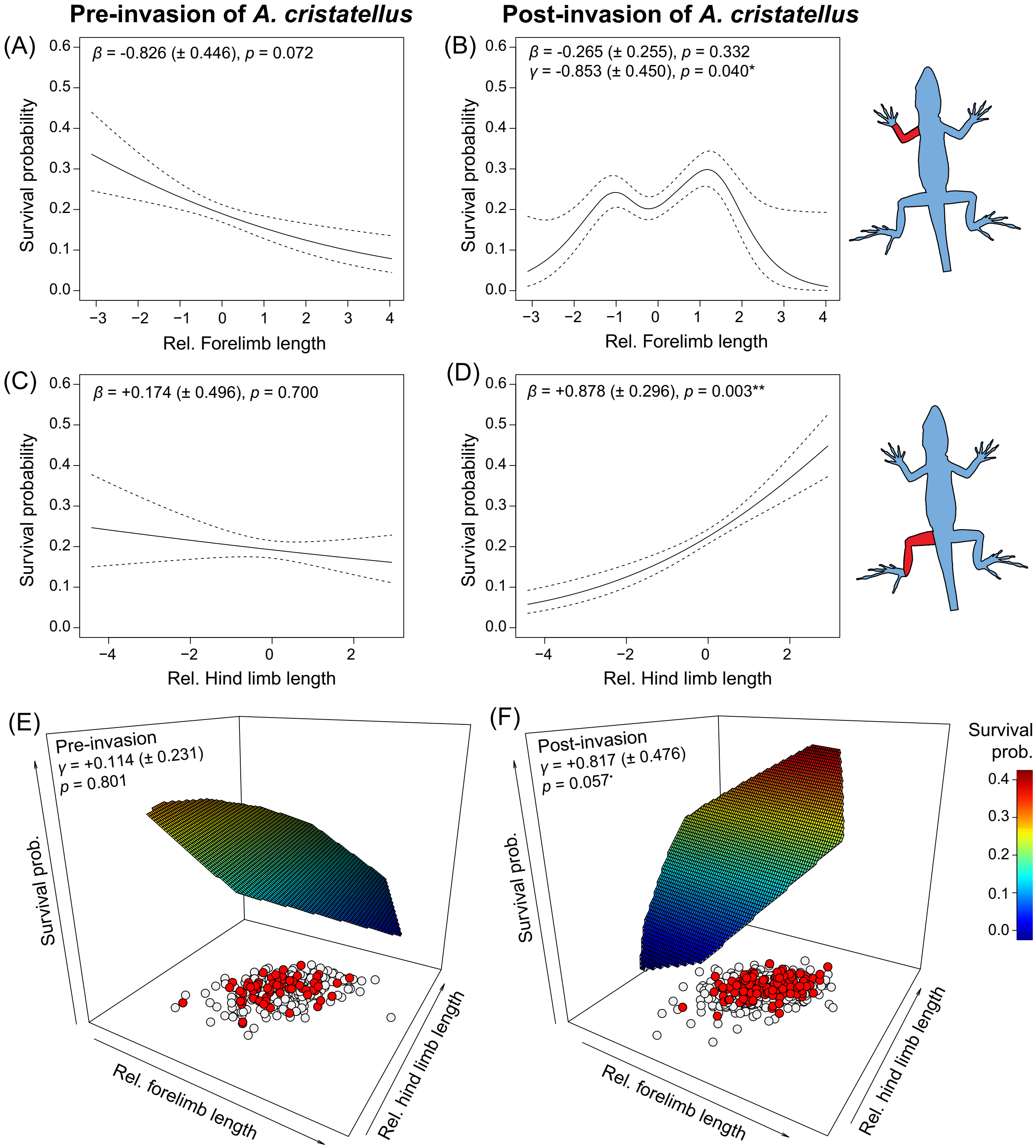

Fig. 3 | Natural selection on limb length during the incipient stages of character displacement. A–D Univariate selection surfaces of relative forelimb and hind limb length for *A. sagrei* before and after invasion by *A. cristatellus*. Solid lines represent the fitted logistic regression model; dashed lines represent ±1 S.E. Relative limb lengths (*x*-axes) represent body size-corrected residuals; values below and above 0 represent relatively smaller and larger limb lengths, respectively. Gray points represent individual lizards; bottom row survival = 0 and higher row survival = 1 (the *y*-axis has been truncated for visual purposes). **E, F** Three-dimensional selection surfaces that estimate survival probability as a function of the correlated relationship between relative forelimb and relative hind limb length; heat colors represent survival probability. All points underneath the selection surfaces represent individual lizards: red points are survivors; unfilled circles are non-survivors. All *p*-values in (**A**–**F**) are from multivariate selection models following Lande & Arnold[89]. $^{\cdot}p < 0.10$, $^{*}p < 0.05$; $^{**}p < 0.01$. All source data are available at: https://doi.org/10.6084/m9.figshare.27165759; data for (**A**–**F**) from file "NatComms_ECD_selection_data".

adaptive evolution hypothesis of limb length in *Anolis* lizards would benefit from common garden experiments that explicitly measure trait heritability under controlled conditions.

Our study provides clear insight into the effect of *A. cristatellus* on habitat use and movement behavior of *A. sagrei* (Fig. 1); in the presence of *A. cristatellus*, *A. sagrei* is more terrestrial than when *A. cristatellus* is absent (Fig. 1). However, the interspecific interactions responsible for driving this pattern of ecological divergence are less clear. Classically, interspecific exploitative competition for limited resources has been considered the primary mechanism responsible for scenarios of this

Table 2 | Natural selection on *Anolis sagrei* after the invasion of *A. cristatellus*

Trait	(i) Selection differential (s)	(ii) Trait fitness optimum (θ)	(iii) Est. fitness at trait optima (ω_{opt})
	Pre / Post	*Pre / Post*	*Pre / Post*
Forelimb	− 0.198 / + 0.102	− 2.997 / + 1.174	0.330 / 0.298
Hind limb	− 0.059 / + 0.253	− 2.896 / + 2.928	0.227 / 0.448

(i) Selection differential (s) represents the trait mean of survivors minus the population trait mean. (ii) Trait fitness optimum (θ) is the trait value of highest fitness; selection was estimated on size-corrected limb traits (negative/positive values represent proportionally smaller/larger trait size than population mean). (iii) Estimated fitness at the trait fitness optimum (ω_{opt}) fitted by cubic splines derived from generalized additive models.

sort that lead to character displacement (i.e., ecological character displacement)[1,2,5]. For example, interspecific competition for limiting food supplies can drive changes in the types of foods consumed and lead to character displacement[42,43]. However, our analysis of diet data did not provide evidence supporting this possibility. It would be valuable for future studies to investigate if competition occurs between these species for other potentially limiting resources, such as the availability of perch types or thermal microsites. Alternatively, agonistic interspecific interactions could be responsible for our observed character displacement via interference competition[44–46]. Our social network data show that individuals of these species occur in close proximity when in sympatry (Fig. 1E), presenting the opportunity for aggressive interspecific interactions. However, the extent to which these species are aggressively interacting, either in frequency or intensity, remains unclear. Future studies of character displacement, particularly those focusing on the *A. sagrei* and *A. cristatellus* system, should explicitly test the roles of various mechanisms to identify the underlying drivers of character displacement in natural populations[16].

As opportunities to study novel contact between similar species in the wild are rare, few convincing case studies exist that have observed character displacement unfolding in the wild (but see refs. 42,47,48). It is possible to establish such situations artificially (e.g., refs. 49–51); however, this approach is not typically feasible at large spatial and temporal scales, especially for terrestrial vertebrates. Non-native species, as we studied here, can offer unique opportunities to study such interspecific interactions in evolutionarily novel scenarios[5,52]. As species are increasingly geographically reshuffled in response to anthropogenic behaviors[53,54], opportunities to study character displacement using non-native species likely will continue to increase.

The theory of character displacement was developed to explain the proximate and ultimate processes that generate repeated patterns of trait divergence in sympatric ecological species. As character displacement is often inferred from a pattern rather than empirically observed as a process[15], the role of divergent natural selection has received surprisingly little empirical support from field studies in the wild. We show here that dramatic shifts in natural selection likely drive a repeated pattern of character displacement across multiple populations.

Methods

Animal procedures were approved by institutional animal care and use committees (IACUC) at Florida International University IACUC #13-070 & #16-059 and Washington University IACUC #20180101. All research was conducted with permission from Florida State Parks Permit #05261635, Miami-Dade Parks Research Permit #208 R, and Florida Fish and Wildlife Permit #EXOT-17-48.

Character displacement: the pattern

Study system. *Anolis sagrei* and *A. cristatellus* are small (40–70 mm snout-to-vent length; Fig. 1A), diurnal lizards that diverged ca. 50–60 Ma and do not hybridize. These species are highly convergent in ecology, morphology, and behavior and classified in the same 'trunk-ground' ecomorph group[19]. *Anolis sagrei* was first recorded in Miami, south Florida, USA, in the mid-1940s[55,56]; *A. cristatellus* in the early 1970s[31,32,56]. *Anolis sagrei* is widespread in Florida, while *A. cristatellus* is limited to Miami-Dade County[21,56]. In their native ranges, both *A. sagrei* and *A. cristatellus* are habitat generalists and occupy similarly structured environments[57,58]. In South Florida, both species occupy a gradient of habitat types from closed canopy forests to urban environments[21,56,59–62] and are estimated to have very similar statewide predicted habitat suitability[63]. We studied ecological resource use (habitat use and diet), movement behavior, and morphology in nine sites across Miami (three allopatric sites per species and three sympatric sites that include both species; Supplementary Tables 1 and 2and Supplementary Fig. 1). All sites contain three other *Anolis* species, all of which are substantially more arboreal than both *A. sagrei* and *A. cristatellus*; the trunk anole (*A. distichus*), the arboreal green anole (*A. carolinensis*), and the giant arboreal specialist *A. equestris*[21,56,64–67]. Although direct predation of *Anolis* lizards was rarely observed during this study, potential predator species were consistent across study communities (J. Stroud *pers. obs.*). Likely common predators include common snakes (e.g., *Coluber constrictor*) and birds (e.g., *Buteo lineatus*, *Cyanocitta cristata*, *Melanerpes carolinus*, *Mimus polyglottos*, *Quiscalus* sp.), all of which were present in each study site (J. Stroud, pers. obs.).

Ecological resource use. We measured two axes of ecological resource use. First, we recorded the habitat use of 1198 lizards (n = 47–221 per species per site; Supplementary Table 3). Specifically, we recorded perch height—the vertical distance from the ground of a perching, undisturbed lizard—which is a primary axis of interspecific habitat partitioning in *Anolis* lizard communities[19]. Second, we analyzed diet extracted from stomach contents (n = 9–15 lizards per species per site; Supplementary Table 3). We identified each sample to the lowest taxonomic level possible and measured to the nearest 0.1 mm under a 10–60x magnification microscope (as in refs. 68,69).

Movement behavior. As perch height observations only represent habitat use for a single time point, we conducted behavioral observations on natural movement and habitat use of 178 *A. sagrei* across all sites (n = 28–31 unique individuals per site; 8–20 mins per lizard, median = 15 mins; total observation time = 2609 min; Supplementary Table 4). As we were most interested in understanding the relationship between movement behavior and habitat use, we recorded the frequency of movements between separate trees (i) across the ground and (ii) above the ground, as well as the frequency of (iii) changes in perching location by a single perch and (iv) movements between perches on the same tree (e.g., from tree trunk to branch, or branch to branch).

Morphology. We measured limb length (forelimb and hind limbs) and body size (snout-vent length [SVL]) using digital calipers (Neiko 01470 A, accurate to 0.01 mm; all measurements by JTS) of both *A. sagrei* (n = 127 allopatry, n = 115 sympatry; n = 23–53 individuals per site; Supplementary Table 3) and *A. cristatellus* (n = 104 allopatry, n = 107 sympatry; n = 24–46 individuals per site).

Statistical analysis. All statistical analyses were conducted in R v4.1.2[70] using RStudio v2021.09.1[71]. We used linear mixed-effects models (*lmer* in R package *lme4*[72]) to test for differences in ecology (perch height and prey size), morphology, and movement behaviors between allopatric and sympatric populations of each species. All models included treatment (i.e., allopatric vs. sympatric) as a fixed effect and site as a random effect to incorporate between-site variation[39,73]. All morphological trait analyses included body size as a covariate. All continuous variables were log-transformed, except perch height and movement behaviors which were square-root transformed (see ref. 39). All model assumptions were checked using the *check_model* function in R package *performance*[74]. We measured niche overlap of prey items (at the family level) using Schoener's proportional similarity index (*D*), using the *niche.overlap* function in the R package *spaa*[75]. Schoener's *D* values > 0.6 infer significant overlap in diet[65].

Population genetic structure Anolis cristatellus. lack population structure throughout our study region having originated from a single source population (Agua Claras/Ceiba region in northeast Puerto Rico[76–78]). Conversely, Floridian *A. sagrei* represents multiple introductions from source populations throughout Cuba and the Bahamas[79]. Thus, we assessed the population structure for 60 *A. sagrei* distributed across our sampling sites. We performed low-coverage whole genome sequencing and aligned our reads to the *A. sagrei* genome (AnoSag2.1)[80] with a mean coverage of 4.62X. Due to our low coverage approach, we incorporated *samtools* genotype likelihoods into our downstream population structure analyses[81].

Interspecific behavioral interactions. To evaluate the strength and frequency of interspecific behavioral interactions in sympatry, we constructed a mixed species social network (site: MHS). We dorsolaterally marked all individuals within our site with a unique alphanumeric code using a non-toxic permanent marker that allowed visual identification using binoculars (*A. sagrei*, $n = 35$ [17 M:18 F]; *A. cristatellus*, $n = 37$ [14 M:23 F]). Following two days of exhaustive capture and marking, the locations of all lizards relative to each other were recorded every 30 minutes for 5 days (50 h total, 0830–1730 each day corresponding with the typical period of *Anolis* activity). Associations between individuals (network 'edges') were classified when two or more individuals were within 3 m of one another, in direct line-of-sight; a conservative estimate of the distance that *Anolis* can visually interact (up to 5.8 m, see ref. 82). We calculated simple-ratio indices between each pair[83] and subsequently each individual's 'weighted degree' of pairwise association using R package *igraph*[84,85]. All observations were made from a distance of > 5 m using binoculars to avoid observer influences on lizard behavior.

Character displacement: the process

Study site. We measured the survival of *A. sagrei* from 2016–2019 on a 6000 m^2 island located within the Fairchild Tropical Botanical Gardens (FTBG) in Miami, Florida, USA (Supplementary Table 1and Supplementary Fig. 1). As with the locations in our comparative analysis, three other *Anolis* species are also present in this community (*A. carolinensis*, *A. distichus*, and *A. equestris*; see ref. 26). These species are all substantially more arboreal than either *A. sagrei* or *A. cristatellus*, are classified as members of different ecomorph groups (*A. carolinensis*, 'trunk-crown'; *A. distichus*, 'trunk'; *A. equestris*, 'crown-giant')[19], and occupy different morphological space[26] and trophic niches in south Florida[65]. No changes in structural habitat or other environmental factors (e.g., other lizard species) occurred during this study, with the exception of the arrival of *A. cristatellus*.

Measuring natural selection. We measured the body size and limb length of male *A. sagrei* ($n = 905$ individuals) using the same methods previously detailed (see Methods subsection '*Morphology*'; all measurements by JTS). Lizards were tagged sub-dermally with small (3 mm) fluorescent tags with unique alphanumeric codes (Northwest Marine Technologies, see ref. 26). We exhaustively measured viability selection every six months and considered all unrecovered tagged lizards as dead[86]. To assess a relationship between survival and limb length, we first visualized the form of selection on size-corrected limb length (residuals from ordinary least squares regression of log-log limb length versus SVL) using cubic splines derived from general additive models (*gam* function in *mgcv* package[87]. To maximize the predictive ability of the fitted GAM, a smoothing parameter was selected to minimize the generalized cross-validation (GCV) score[88]. As survival data are binary, all GAMs were processed as binomial with a logit link function[88].

After visualizing the forms of selection, we estimated linear (β) and nonlinear (γ) selection gradients as appropriate (Fig. 3). All variables were scaled to a mean of 0 and a standard deviation of 1. To estimate selection gradients (and associated standard error), we calculated partial regression coefficients from ordinary least squares multiple regression using relative survival as the response variable[89]. The forelimb, hind limb, and body length (SVL) were all included in the model. Statistical significance was estimated by logistic regression[89] with a link = 'logit' function as survival data are binary[88]. Selection coefficients (and associated standard error) for quadratic and correlational terms were doubled[90]. Linear coefficients and *p*-values were estimated from models only including linear terms; quadratic coefficients were estimated from full models including all linear, quadratic, and correlational terms. As survival was estimated for two consecutive sampling periods, both before and after *A. cristatellus* invasion, we included the sampling period as a random effect. Three-dimensional fitness surfaces (Fig. 3E, F) were visualized with thin-plate splines to fit the data by generalized cross-validation (*Tps* function in *fields* package[91]).

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

All ecological and morphological data generated in this study have been deposited in Figshare: https://doi.org/10.6084/m9.figshare.27165759. Raw sequence data for our project is archived under Bioproject PRJNA1180189. Sequence alignment was performed using the AnoSag2.1 genome assembly (NCBI genome accession: JANCLY0100000000; reference number GCF_025583915.1; Bioproject PRJNA783271 [https://www.ncbi.nlm.nih.gov/bioproject/783271]).

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Author contributions

J.T.S. conceived and designed the study. J.T.S., S.T.G., R.J.P.H., S.T., and M.L.Y. collected data. J.T.S. analyzed the data. M.L.Y. analyzed the genetic data. J.T.S. wrote the manuscript with input from all co-authors: S.T.G., R.J.P.H., S.T., M.L.Y., K.J.F., and J.B.L.

Competing interests

The authors declare no competing interests.

Additional information

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Correspondence and requests for materials should be addressed to James T. Stroud.

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