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Citation

Herrmann, Nicholas Carl. 2021. Competition, Character Displacement, and Ecological Release in Anolis lizards. Doctoral dissertation, Harvard University Graduate School of Arts and Sciences.

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Competition, Character Displacement, and Ecological Release in *Anolis* lizards

Nicholas Carl Herrmann

July 2021

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Competition, Character Displacement, and Ecological Release in *Anolis* lizards

Abstract

The addition or subtraction of species in a community can alter the ecology and evolution of resident species. As human-mediated introductions and extinctions have become commonplace, understanding the consequences of changing species interactions is more important than ever. Here, colleagues and I investigate two closely related processes that connect competition between species to evolutionary change: ecological character displacement and ecological release.

In Chapter 1, we evaluate interactions in the field between the arboreal lizards *Anolis carolinensis* (the native green anole) and *Anolis sagrei* (the introduced brown anole) in Florida. We show that brown anoles are more aggressive and less flighty than green anoles, suggesting a competitive asymmetry.

Previous work on islands in Florida showed that green anoles perch higher and adaptively evolve larger adhesive toepads in the presence of brown anoles. In Chapter 2, we revisit these same islands to test hypotheses about how this process of competition-driven habitat and morphological divergence, termed ecological character displacement, varies across space and time.

In Chapter 3, we explore historical and recent trends in the study of ecological release, a phenomenon often described as the opposite of ecological character displacement. We show that while ecological release was originally defined as niche expansion following a reduction in interspecific competition, current definitions are broad and highly varied. Viewing this

development as a potential impediment to clear communication and hypothesis testing, we suggest a consensus definition for ecological release, highlight the various ways the process can unfold, and make suggestions for future studies of ecological release and its evolutionary implications.

In Chapter 4, we experimentally induce ecological release of green anoles from brown anoles, monitoring individual and population habitat use along three niche axes (perch height, perch diameter, and lateral movement between perches) for two generations. Our results suggest that that the eco-evolutionary dynamics of ecological release in nature need not be solely inferred, because experiments can observe them directly at level of individuals, across generations, and along multiple niche axes.

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Acknowledgements

The work described herein would not have been possible without help from many people. Thanks to everyone who helped with data collection or provided logistical support in the field. Special thanks to Michael Boyle, Chelsea DeCambre, Carol Herzog, Aaron Hochberg, Dylan Gavagni, and Debbie and Kenny Langley. Extra special thanks to current and former staff at the Florida Department of Environmental Protection's Aquatic Preserve Program, including Matthew Anderson, Irene Arpayaglou, Emily Dark, Kirk Fusco, and Barchan Rogers – I've been repeatedly overwhelmed by your generosity. Multiple sources provided funding for this work, including the National Sciences Foundation, the National Geographic Society, the Sigma Xi Scientific Research Honor Society, the Harvard Museum of Comparative Zoology, and the Harvard Chapman Fund.

The Department of Organismic and Evolutionary Biology is full of kind, helpful, and smart people who have supported me over the past six years. Thanks to the administrative staff for helping me hundreds of times, with a special thanks to Jared Hughes for help planning fieldwork. I've enjoyed my interactions with faculty and would like to name Robin Hopkins, Elena Kramer, and Naomi Pierce in particular for the consistent, positive influence they've had on my time in OEB. The cohort of OEB students I began graduate school is a dream team of exceptional individuals. I'm honored to have been among your ranks and eager to see all the ways in which you make the world a better place. David Haig became my PhD advisor halfway through my dissertation and has been resolutely supportive. Thank you, David, and everyone in the Haig group for making my second home in the department a welcoming and intellectually stimulating space.

My original PhD advisor Jonathan Losos left Harvard, but he never stopped being my mentor. Jonathan, thank you for everything, including assembling a lab of amazing people. I've benefited so much from the friendship and mentorship of current and former Losos lab graduate students and post-docs. Special thanks to Anthony Geneva, Ambika Kamath, Graham Reynolds, and Yoel Stuart – my brain is strong from your wisdom, and my heart is full from your generosity. Sofia Prado-Irwin, you are super cool, and I'm grateful for your friendship.

Lastly, I have amazing friends and family who are beacons of love and positivity. Thank you Gail, Larry, Justin, Ashley, Simon, and Elliott. Thank you Mom, Dad, JH, Step, and Jen. Thank you Oma. And thank you Alex – you are my rock.

Introduction

If you're lucky enough to know a place in the outdoors for many years, you may notice that the plants and animals there change over the course of your lifetime. The speed and intensity of changes vary substantially across the natural world, but that they occur is biological fact. Human actions are responsible for some of the most dramatic of these changes to natural communities. In some cases, the human impacts are direct and obvious, such as when a species is hunted to local extinction. People add species to ecosystems as well, sometimes intentionally, and sometimes unintentionally, as a byproduct of the pet trade or shipping commerce. Humans also alter community composition indirectly by modifying the qualities of a habitat through agriculture, urbanization, and climate change. To summarize, we live in a world where species get added to and subtracted from ecological communities all the time. As human domination of the planet has intensified, so too have the frequency and magnitude these events.

What happens to the residents of an ecological community when species are added or subtracted? For decades, this question has been central to the field of community ecology, defined as study of the organization and functioning of communities, which are assemblages of interacting populations of the species living within a particular area or habitat. Early experiments showed ways in which the distribution and behavior of resident species changed when they were relieved of pressure from competitors (e.g. Connell 1961) or predators (Paine 1966), setting the stage for a generation of field biologists who would intentionally add or subtract species from natural communities and measure the consequences. Yet the consequences they were interested in were largely *ecological* – researchers would measure the features of a population such as its size, the habitats it occupied, and the resources it consumed, to determine how it was being affected by whatever species had been added or removed.

The notion that interactions like competition or predation might also drive *evolutionary* changes, such as heritable shifts in the physical features of a species, has also been widely accepted for decades. However, such evolutionary changes were seldom tested in experiments because they were thought to occur too slowly to measure directly. Indeed, Charles Darwin himself, an avid experimentalist, never tested his famous theory of evolution by natural selection because he thought the process was not observable within a human lifetime. But that is false. Sometimes evolution does occur slowly, but sometimes measurable changes to heritable traits can be detected within just a few generations. When such rapid evolution can be tied to say, the introduction of a new competitor or the extinction of a longstanding predator, we have added another layer of complexity to the question, what happens to the residents of an ecological community when species are added or subtracted? At this point, the question extends beyond the bounds of classic community ecology and enters the purview of the field of evolutionary ecology. As its name suggests, evolutionary ecology lies at the intersection of ecology and evolutionary biology. It is explicitly concerned with the evolutionary effects of species interactions.

In this dissertation, I use an evolutionary ecologist's lens to explore the question, what happens to the residents of an ecological community when species are added or subtracted? Specifically, I focus on two species of arboreal lizard in the genus *Anolis* which co-occur in Florida, the longtime resident *Anolis carolinensis* (green anole), and more recently introduced *Anolis sagrei* (brown anole). I have studied these species exclusively in the field, using a mix of experimental manipulations and serendipitous natural community changes to directly observe eco-evolutionary processes that are often inferred rather than seen in action. How do these species interact? The short answer is that they compete, though I explore this interaction in depth in Chapter 1. What happens to naïve green anoles when brown anoles arrive? The answer is ecological character displacement, a process I study in Chapter

2. What happens to green anoles if the brown anoles they have been living with are removed? The answer is a process called ecological release, which is the topic of Chapters 3 and 4.

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Chapter 1

Asymmetric interference competition and niche partitioning between native and invasive *Anolis* lizards

This chapter is published and should be cited as follows:

Culbertson, K. A., & Herrmann, N. C. (2019). Asymmetric interference competition and niche partitioning between native and invasive *Anolis* lizards. *Oecologia*, 190(4), 811-820.

Associated data and R script are available from GitHub (<https://github.com/NCHerrmann/interference/>)

1.1 Summary

Species can compete both directly via aggressive encounters (interference) and indirectly through their shared use of a limited resource (exploitation). Depending on the circumstances, interference, exploitation, and their interplay can either lead to competitive exclusion or drive niche partitioning to maintain species coexistence. Thus, understanding species coexistence in nature requires accurately identifying the mechanisms that contribute to competition among the species in question. In the southern United States, the native lizard *Anolis carolinensis* becomes more arboreal in the presence of the invasive *Anolis sagrei*, resulting in highly consistent vertical habitat partitioning where the species co-occur. These species have been thought to largely ignore each other and engage only in exploitative competition for shared arthropod prey. To test for the presence and consequences of direct interference, we conducted behavioral trials in the field, introducing a heterospecific male intruder to individuals of both species. We find that interference competition is asymmetric in favor of *A. sagrei*, which are more likely to display and less likely to retreat than *A. carolinensis*. Concordant with their arboreal tendencies, male *A. carolinensis* also trend toward retreating upward more often than

expected by chance. These asymmetries are prevalent despite the almost complete absence of physical attacks, suggesting that interspecific signaling and avoidance behavior by *A. carolinensis* resolve most potential conflicts before they escalate to combat. Our results highlight the potential for direct interference more subtle than frequent outright combat to structure communities, and *Anolis* assemblages in particular.

1.2 Introduction

Niche partitioning facilitates the coexistence of competitors that divide available resources by separating along one or more niche dimensions (e.g. diet, habitat, activity time; Schoener 1974, Chesson 2000). One mechanism that can maintain interspecific niche partitioning is interference competition, during which individuals engage directly via aggressive encounters or physical crowding (Blaustein and Risser 1974, Morse 1974, Carothers and Jaksić 1984, Jenssen et al. 1984; Ziv et al. 1993, Robinson and Terborgh 1995, Rychlik and Zwolak 2006, Reynolds and Rajaniemi 2007; Kimura and Chiba 2010). Aggression is common among animal species that overlap substantially in resource use (Peiman and Robinson 2010) and can induce niche shifts and character displacement in both behavioral and morphological traits (Adams 2004; Grether et al. 2009, 2013, 2017). As an alternative, or in addition to direct interference, competition can occur indirectly when coexisting species both deplete a limited resource, even if their use of said resource is separated spatially or temporally (termed exploitative competition). Although exploitative competition has historically received more attention than interference competition as a driver of niche shifts and character displacement (Schluter 2000, Grether et al. 2009, Stuart and Losos 2013), both interference and exploitative competition are common in nature (Schoener 1983). Theory predicts that their joint contributions to species coexistence depend on several factors, including whether resources fluctuate (Armstrong and McGehee 1976, 1980), whether interference is costly (Amarasekare 2002), and whether habitat heterogeneity permits species to find

refuges from superior competitors (Amarasekare 2003). Evaluating these predictions requires accurately identifying the mechanisms that contribute to empirical examples of niche partitioning.

Interspecific competition is often asymmetric, with the effect of one species on the other's fitness being greater than the inverse (Lawton and Hassell 1981, Connell 1983, Schoener 1983). Competitive asymmetries can result from species differences in resource exploitation efficiency (Tilman 1982, Morin and Johnson 1988, Byers 2000), dominance through direct interference (Morse 1974, Robinson and Terborgh 1995, Rychlik and Zwolak 2006; Kimura and Chiba 2010), or both (Case and Gilpin 1974, Persson 1985, Human and Gordon 1996, Lach 2005). In a homogenous environment with limited resources, a competitively superior species will ultimately extirpate its inferior, but niche partitioning in a heterogeneous environment can dampen the intensity of interspecific competition and facilitate species co-existence (Chesson 1991, Leibold 1995, Chesson 2000, Amarasekare 2003). Empirically, this occurs often via the partitioning of physical space (Schoener 1974, 1986, Robinson and Terborgh 1995, Grether et al. 2013, Freshwater et al. 2014).

Lizards in the genus *Anolis*, the anoles, are a well-studied example of closely related competitors that exhibit interspecific habitat partitioning (Schoener 1975, Losos 2009). In the United States, allopatric populations of the American green anole, *Anolis carolinensis*, are generalists in their habitat use (Collette 1961), although they are morphologically classified as “trunk-crown” anoles because their relatively short limbs are well-adapted for locomotion on the thin branches that are prevalent in the forest canopy (Losos and Sinervo 1989; Losos 1990, 2009). Following the invasion of the Cuban brown anole, *A. sagrei*, a “trunk-ground” ecomorph well-adapted for locomotion on broad tree trunks (Losos and Sinervo 1989; Losos 1990), green anoles adopt higher average perch heights more typical of trunk-crown anoles, resulting in highly consistent interspecific vertical habitat partitioning where the species co-occur (Collette 1961, Edwards and Lailvaux 2012, Stuart et al. 2014). Invaded *A. carolinensis* populations also undergo morphological character displacement by evolving larger toepads with more

adhesive scales, a perceived adaptation concordant with their increased arborealism (Glossip and Losos 1997, Stuart et al. 2014).

Niche partitioning between *A. carolinensis* and *A. sagrei* has been thought to arise from exploitative competition for shared arthropod prey, as both species are considered generalist insectivores (Campbell 2000, Turnbough 2016). In other words, heterospecifics are thought to largely ignore each other but are differentially successful at capturing prey along the continuum of vertical space, leading to habitat partitioning. Being trunk-ground specialists, *A. sagrei* may be highly efficient at capturing prey near the ground but struggle to do so on thin branches high in the canopy, where the trunk-crown anole *A. carolinensis* can move around with relative ease. However, indirect evidence suggests that asymmetric interference competition also contributes to the vertical displacement of *A. carolinensis* following *A. sagrei* invasion. During staged laboratory encounters between heterospecifics, aggressive displays (dewlap [throat fan] extensions, pushups, and headbobs) are relatively common and more so in *A. sagrei* than in *A. carolinensis*, even though physical combat is rare (Tokarz and Beck 1987, Edward and Lailvaux 2013). To date, however, interference competition between these species has not been studied in the field.

In this study, we used tethered intruder trials (Stamps 1977, 1978; Hess and Losos 1991; Reedy et al. 2017) to investigate whether asymmetric interference competition between *A. carolinensis* and *A. sagrei* occurs in the field and thus could potentially contribute to their interspecific niche partitioning. If so, it would be the first thoroughly documented example of interference competition among anoles whose morphology clearly separates them into distinct ecomorph classes (*A. carolinensis*: trunk-crown ecomorph; *A. sagrei*: trunk-ground ecomorph). We hypothesized that interference competition is asymmetric and favors the invasive *A. sagrei* over the native *A. carolinensis*. In accordance with this hypothesis, we predicted the following four behavioral outcomes in tethered intruder trials: 1) *A. carolinensis* would be less likely to display than *A. sagrei*; 2) attacks would be rare overall and less likely

to come from *A. carolinensis* than *A. sagrei*; 3) *A. carolinensis* would be more likely to retreat than *A. sagrei*; and 4) among lizards that retreat, the trunk-crown ecomorph *A. carolinensis* would be more likely to retreat upward than the trunk-ground ecomorph *A. sagrei*.

1.3 Methods

Study Area

We conducted this study on two low-lying dredge spoil islands in Florida's Indian River Lagoon, BC44B (27°56'29.18"N, 80°31'20.69"W; area = 1.88 ha) and BC47 (27°54'34.02"N, 80°30'27.27"W; area = 1.61 ha) from 18-July-2017 to 29-July-2017. The islands contain sympatric populations of *A. carolinensis* and *A. sagrei* (Figure 1.1) at relatively high densities. The exact duration of sympatry is unknown, but *A. sagrei* is present on almost every island within 10 km of BC44B and BC47 (NCH personal observation), and many nearby islands in the lagoon have contained both species for decades (Campbell 2000). The islands are similarly vegetated, with a mix of closed-canopy stands and more open, shrubby or scrub areas. Both islands have an abundance of tall trees, most commonly Australian pine (*Casuarina* sp.), Brazilian pepper (*Schinus terebinthifolia*), red (*Rhizophora mangle*) and black (*Avicenna germinans*) mangroves, and cabbage palms (*Sabal palmetto*).

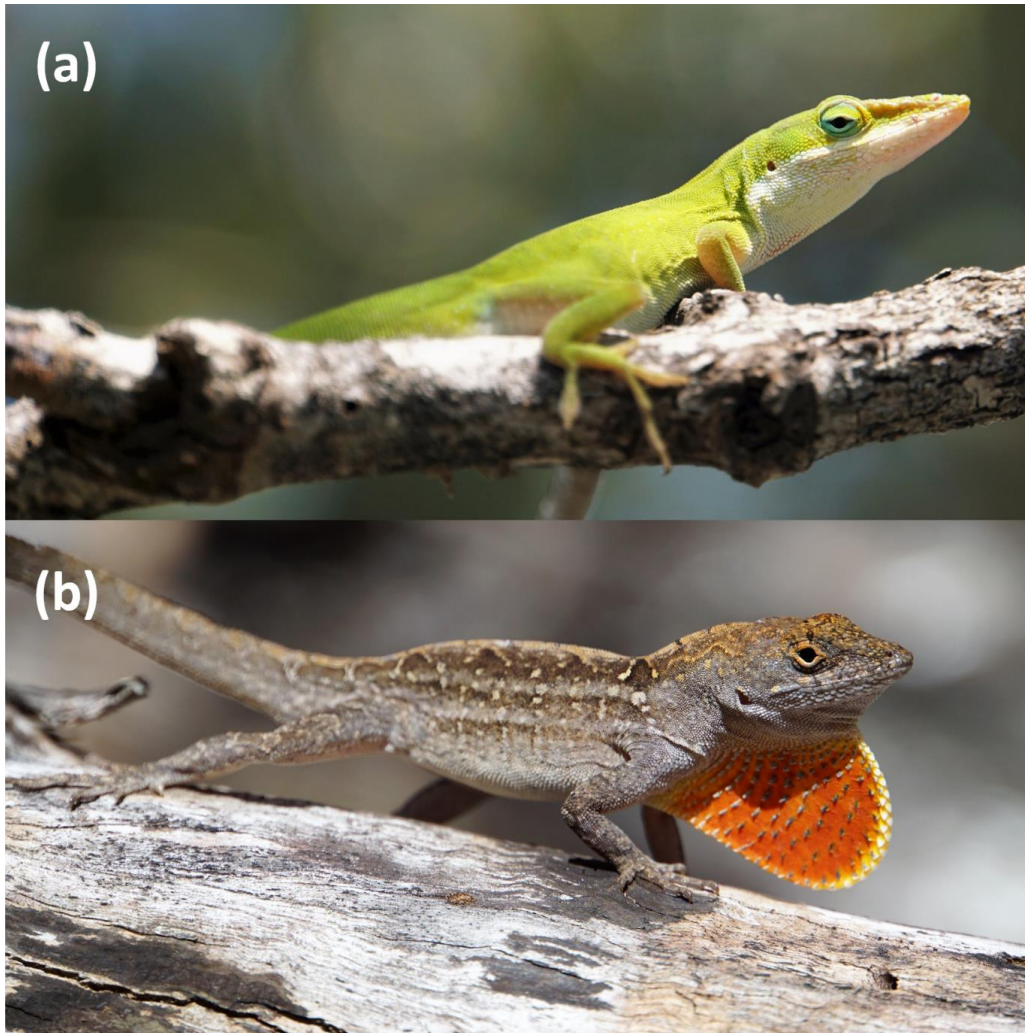


Figure 1.1 Anoles photographed on a Floridian dredge spoil island (a) *Anolis carolinensis* male (b) *Anolis sagrei* male with dewlap extended. Photo credit: NCH

Tethered Intruder Trials

We completed 92 tethered intruder trials in which a heterospecific male intruder was introduced to a focal lizard (focal lizards: 28 male *A. carolinensis*, 34 male *A. sagrei*, 30 female *A. carolinensis*). Intruders came from the other island (i.e. focal lizards on BC44B were presented an intruder from BC47 and vice versa), ensuring that each focal lizard had never encountered the specific individual chosen as its intruder. All intruders were captured in the morning, kept in breathable cloth

bags throughout the day, used in 1-3 trials at random but with at least two hours between trials, marked after use with a non-toxic marker to avoid recapture, and returned to their point of initial capture at the end of the day.

We chose to use only male intruders for two reasons. First, males are probably more likely than females to initiate interspecific interactions because male anoles are more mobile and more aggressive than females (Schoener and Schoener 1982, Jenssen and Nunez 1998, Calsbeek 2009, Herrmann et al. 2018, Kamath and Losos 2018). Second and more importantly, male *A. sagrei* tend to perch higher than females (Lister 1976, Schoener 1968, Schoener and Schoener 1971), making the former more likely to interact with both male and female *A. carolinensis*, which perch even higher (Collette 1961, Edwards and Lailvaux 2012, Stuart et al. 2014). On Floridian spoil islands in particular, female *A. sagrei* perch so low that they are largely non-overlapping with both male and female *A. carolinensis* (Campbell 2000). Thus, although female *A. sagrei* display interspecific aggression in the laboratory and may interfere with heterospecifics frequently during the incipient stages of invasion (Edwards and Lailvaux 2013), in longer standing areas of sympatry (such as our study sites) the habitat use of female *A. sagrei* likely limits their opportunities to directly interact with *A. carolinensis*. This is also the reason that we elected not to conduct trials with *A. sagrei* females as focal lizards.

Behavioral trials occurred between 8:30 and 16:00 during dry weather and were videotaped for subsequent analysis. We walked slowly around the island, initiating trials only with focal lizards spotted from at least five meters away that were undisturbed by our presence and perched in a location where they could choose to move either up or down (i.e. not on the ground or at the top of a bush or tree). We set up the video camera no closer than 4 meters from the focal lizard and then placed an intruder one meter away using a 3.6-m fishing pole. Intruders were tethered around the waist with black fishing line and given enough slack to move freely once they were placed. Because we were explicitly interested in the movement direction of retreating lizards, we alternately placed intruders above or below the focal

lizard to avoid biasing movement in the vertical plane. Trials were terminated either when the focal lizard retreated, either lizard attacked (in which case the intruder was removed before the lizards could engage in physical combat), or five minutes had elapsed. We moved the video camera as needed during the trial to maintain visibility (but never closer than 4 meters). After the trial concluded, we captured each focal lizard, recorded its snout-vent length (SVL) in millimeters, marked it with a non-toxic marker to prevent reuse in a subsequent trial, and released it at its exact point of capture. Ten male *A. carolinensis* and two male *A. sagrei* evaded capture, so we were unable to measure and mark these individuals. We also recorded the SVL of the intruder, the focal lizard's perch height at the start of the trial, and whether any other anoles were present within a 3-m radius of the trial.

Video Analysis

We used JWatcher version 1.0 software (Blumstein et al. 2006) to measure the exact duration of each trial and quantify the behavior of both focal lizards and intruders. We set out to evaluate asymmetries in interspecific aggression based not only on how frequently individuals from each species attacked heterospecifics, but also how often they displayed, how often they retreated, and in what direction they retreated. To that end, we recorded all movements, headbobs, pushups, and dewlap extensions made by both focal and intruding lizards. We also categorized the end result of each trial based on whether the focal lizard attacked, retreated, or neither. We defined a retreat as focal lizard movement away from the intruder, without returning, of at least two meters or until it could make no further progress in its chosen direction (e.g. at the top of an isolated tree if retreating upward). We classified the direction in the vertical plane of each retreating lizard as up, down, or neither. Retreats that were categorized as up or down required a clear displacement of at least one vertical meter from the animal's starting location regardless of the extent of horizontal movement. For the twelve trials involving male focal lizards that evaded capture, we analyzed frames from the video using the software ImageJ 1.50i (Rasband 1997) in attempt to compare the SVL of the focal lizard and the intruder. We

confirmed for six of these trials whether the intruder was definitively larger or smaller than the focal lizard.

Statistical Analyses

We evaluated our hypotheses using only the behaviors of focal lizards as response variables. The behaviors of tethered intruders were not used as response variables in any statistical model.

To test for species-specific differences among focal males, we used generalized linear models (GLMs) with various behaviors of interest as response variables. These behaviors included whether the lizard displayed (binary), the number of displays per minute (continuous), and whether the lizard retreated (binary). Fixed effect predictors in each model included species identity (binary), island of origin (binary: BC44B or BC47), whether the intruder was larger than the focal lizard (binary), whether the intruder was active or inactive (binary: either moved or displayed during the trial or didn't), the placement of the intruder (binary: above or below the focal lizard), and height of the focal lizard at the start of the trial (continuous). Models with display-related response variables also included the following additional predictors: the presence/absence of conspecifics (binary) and the trial duration (continuous). We chose these predictors assuming that each might independently explain variation in focal lizard behavior. Although predictors other than species identity are included essentially as covariates, we occasionally discuss their explanatory power in fitted models. However, we exercise caution in drawing conclusions about the causal influence of predictor variables that we did not manipulate. We excluded from analysis any trials with missing data, namely trials in which the relative body size of the focal lizard was unknown (6 of the 28 trials with a male *A. carolinensis* focal lizard).

The movement direction of retreating lizards could not be analyzed using a GLM because so few *A. sagrei* retreated, so we used an exact one-tailed binomial test to evaluate the hypothesis that retreating *A. carolinensis* males were biased toward retreating upward. Attacks could not be analyzed statistically because so few occurred.

We tested for differences in the response of male versus female *A. carolinensis* to male *A. sagrei* intruders using a set of GLMs similar to those described above. Response variables included whether the lizard retreated (binary) and whether retreating lizards retreated upward (binary). Predictors for these models were as described above with two exceptions: focal lizard sex was substituted for species identity and the body size predictor was dropped (because all male *A. sagrei* intruders were substantially larger than all female *A. carolinensis* focal lizards).

To estimate effects and the uncertainty around those effects, we used a Bayesian modeling framework implemented through the *rstanarm* package (version 2.15.3) in R version 3.4.1 (R Development Core Team 2017). All estimated model parameters were assigned weakly non-informative priors (tripling their variance did not qualitatively change our results). Posterior distributions of model parameters were estimated from 2000 samples from each of four independent Markov chains (with 2000 iterations of warmup). Convergence was always achieved, as assessed by a potential scale reduction factor of one and high effective sample sizes.

We evaluated species-specific differences among males and sex-specific differences among *A. carolinensis* by generating posterior predictions for each response variable at the mean values of all other predictors. When species- or sex-specific 95% credible intervals did not overlap, we rejected the null hypothesis that species or sexes behave similarly.

Although we present only the results of the models described above, we fit several additional models to evaluate the robustness of our conclusions to various modeling choices. Primary among these was the choice to treat all trials as statistically independent even though some intruders were used more than once. We justify this choice on two grounds. First, we re-ran all models using only the subset of trials in which an intruder was used for the first time. Posterior medians from these subset models were extremely similar to those from the full models, but predictions had wider 95% credible intervals due to reduced sample sizes. Second, various aspects of the intruder's biology and behavior, such as

body size and activity level, were included in all models as predictors to account for some of the most obvious ways in which a specific intruder might influence the behavior of a focal lizard. Data and an annotated R script are available on GitHub (<https://github.com/NCHerrmann/interference/>).

1.4 Results

Male *A. sagrei* were more likely to display than male *A. carolinensis*, as indicated by non-overlapping 95% CIs for the probability of display (Figure 1.2a), although species-specific display rates were less distinct (Figure 1.2b). Focal lizards displayed in over two-thirds of all trials, but only two attacks occurred, both by male *A. sagrei* (Table 1).

Despite the rarity of attacks, male *A. carolinensis* were substantially more likely to retreat than male *A. sagrei* (Figure 1.2c). Male *A. sagrei* tended to have a greater SVL than male *A. carolinensis*, resulting in more trials with a larger *A. sagrei* (Table 1.1), but relative body size had almost no explanatory power in this model (nor in any model); smaller focal *A. sagrei* males never retreated (0 of 6 trials) and larger *A. carolinensis* males retreated often (5 of 7 trials). Retreating *A. carolinensis* males ($n = 22$) retreated upward 68% of the time, marginally more often than expected by chance ($P = 0.068$, exact one-tailed binomial test). This tendency was not influenced by the placement of the intruder, as intruder placement had almost no explanatory power in any model.

The probability of retreating for female *A. carolinensis* facing a heterospecific male was nearly identical to that of male *A. carolinensis* (Figure 1.3a). Unlike males, retreating females ($n = 23$) showed no directional preference (Table 1.1, Figure 1.3b).

Other than species identity, no predictor variable in any model had a 95% CI that did not span zero, suggesting that these variables had little to no explanatory power for any behavioral outcome.

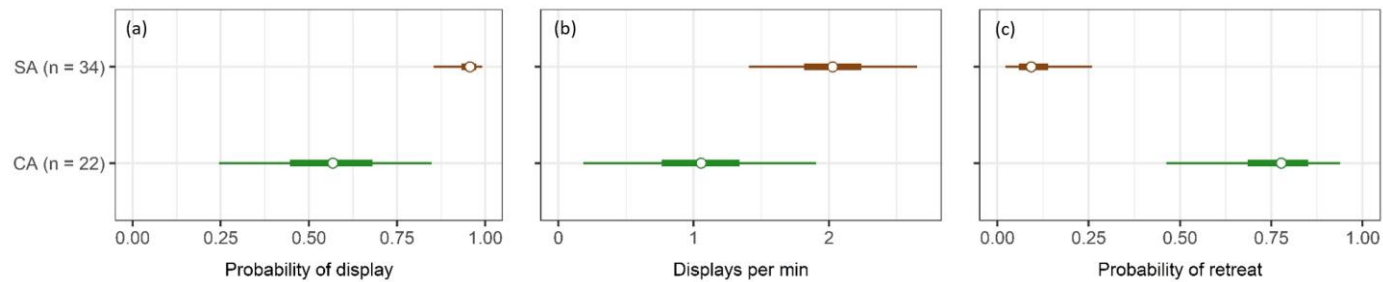


Figure 1.2 Posterior predictions for the (a) probability of display, (b) display rate, and (c) probability of retreat of male *Anolis sagrei* (SA) and male *Anolis carolinensis* (CA) when presented with a heterospecific intruder. Posterior medians and credible intervals (CIs) were evaluated at the mean values for all other predictor variables included in each model. Hollow circles = median, thick bars = 50% CIs, thin bars = 95% CIs

Table 1.1 Descriptive statistics summarizing tethered intruder trials, including both unmanipulated environmental variables and focal lizard behavioral responses. Percentages represent the proportion of trials to which each descriptor applies.

Focal Lizards	Number of Trials	Mean Duration in Minutes (SD)	Mean Perch Height in cm (SD)	Intruder SVL > Focal SVL ^a	Active Intruder ^b	Conspecifics Present	Focal Attacked	Focal Displayed	Focal Displays per minute	Focal Retreated	Proportion of Retreats that were Upward
Male <i>A. sagrei</i>	34	3.3(1.3)	84(58)	18%	68%	44%	6%	91%	2.1	9%	33% (1/3)
Male <i>A. carolinensis</i>	28	3.3(1.4)	274(133)	68% ^c	54%	11%	0%	54%	1.4	79%	68% (15/22)
Female <i>A. carolinensis</i>	30	3.6(1.6)	205(125)	100%	50%	10%	0%	50%	0.5	77%	52% (12/23)

^aSVL = snout-to-vent length

^bMeaning the intruder moved or displayed

^cSix trials in which the focal lizard evaded capture and its relative SVL could not be determined from video analysis were excluded from all analyses comparing male *A. sagrei* to male *A. carolinensis*

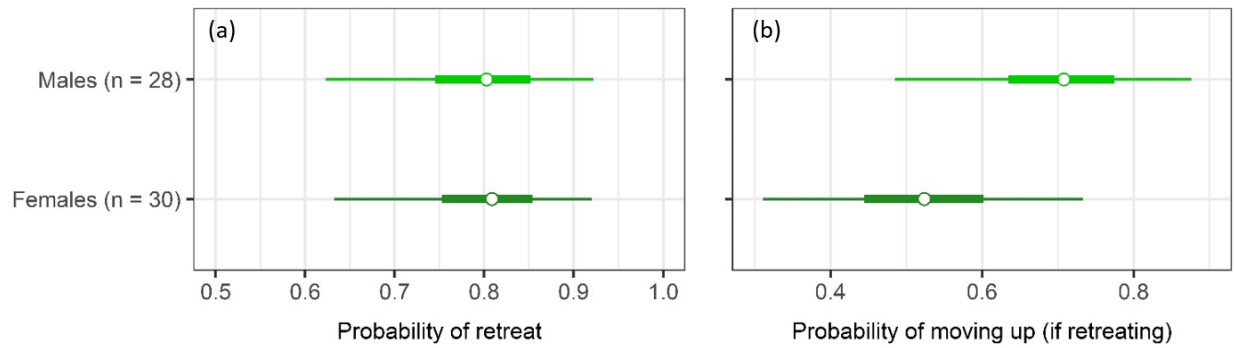


Figure 1.3 Posterior predictions for the (a) probability of retreat and (b) probability of moving upward for male and female *Anolis carolinensis* when presented with a male *Anolis sagrei* intruder. Posterior medians and credible intervals (CIs) were evaluated at the mean values for all other predictor variables included in each model. Hollow circles = median, thick bars = 50% CIs, thin bars = 95% CIs

1.5 Discussion

Interspecific aggression is less common and often less intense than intraspecific aggression, yet it can still be an important force in structuring communities (Ord and Stamps 2009, Peiman and Robinson 2010, Grether et al. 2017). Even in the absence of frequent physical combat, the outcomes of aggressive signaling interactions, including avoidance behaviors such as retreating, can maintain dominance relationships (Rowell 1966, 1974, Kaufmann 1983) and interspecific habitat partitioning (Morse 1974, Robinson and Terborgh 1995). Consistent with prior laboratory studies (Tokarz and Beck 1987; Edwards and Lailvaux 2013), we observed very few interspecific attacks between *A. carolinensis* and *A. sagrei* in the field. Nonetheless, the outcomes of our staged behavioral interactions suggest that the invasive *A. sagrei* is dominant over the native *A. carolinensis*. In accordance with our predictions, *A. carolinensis* are less likely to display and more likely to retreat than *A. sagrei* at the end of an interspecific encounter. Male *A. carolinensis* also trend toward retreating upward more often than

expected by chance. These results suggest that the role of asymmetric interference competition in maintaining niche partitioning between these species has been previously overlooked.

Despite evidence that larger species are often competitively dominant in nature (Schoener 1983, Persson 1985, Shelley et al. 2004, Chock et al. 2018) and that body size positively correlates with aggression in male *A. carolinensis* and *A. sagrei* in the laboratory (Edwards and Lailvaux 2013), in our study, relative SVL accounted for essentially none of the variation in submissive retreat behavior. Because male *A. sagrei* tend to outsize male *A. carolinensis* at our study sites, we conducted fewer trials with larger *A. carolinensis* and smaller *A. sagrei*. Even so, dominance can be mediated by differences in traits other than body size (e.g. Chucholl et al. 2008, Hongo and Okamoto 2013), the importance of which may be lost outside of natural contexts.

In our study system, interspecific differences in ecomorphology and behavior may pre-dispose *A. sagrei*, even when they are smaller, to dominate direct encounters in the microhabitats where interactions most frequently occur. *A. sagrei* often demonstrate high site fidelity for weeks at a time during the summer breeding season (Schoener and Schoener 1982, Calsbeek 2009; but see Kamath and Losos 2017, 2018). In accordance with this tendency, almost all *A. sagrei* that we observed remained on their starting perch and displayed when presented with a male *A. carolinensis* intruder. Due to their trunk-ground ecomorphology, *A. sagrei* can sprint faster than *A. carolinensis* on wide perches such as tree trunks (Losos and Sinervo 1989, Losos 1990). Most of our trials occurred below three meters where wide perches are relatively abundant. Because *A. carolinensis* (a trunk-crown ecomorph) are better adapted than *A. sagrei* to maintain balance on leaves and narrow branches (Losos and Sinervo 1989, Losos 1990), perhaps the apparent dominance hierarchy observed in this study would be reversed if trials were conducted in the canopy, where *A. sagrei* might struggle to gain sure footing. However, *A. sagrei* rarely perch above three meters even when they are in allopatry (Lister 1976), suggesting that the unmanipulated perch heights at which we conducted trials represent the heights at which these two

species are most likely to interact, and that the canopy may serve as a spatial refuge for *A. carolinensis* from direct interference by *A. sagrei* (Amarasekare 2003).

Although direct interference appears to contribute to niche partitioning between *A. carolinensis* and *A. sagrei*, whether the behavior of either species is adaptive remains unknown. *A. sagrei* is arguably the most successful anole invader of the past 200 years, having established itself on multiple islands and continents already occupied by other *Anolis* species (King and Krakauer 1966, Savage and Bolaños 2009, Powell et al. 2011, Oliveria et al. 2018). A tendency to display aggression toward potential heterospecific competitors may contribute to its success as an invader (Holway and Suarez 1999). Even so, baseline aggression in this context would be more exaptive (*sensu* Gould and Vrba 1982) than adaptive. For *A. carolinensis*, individuals from allopatric populations may behave differently than individuals that co-occur with *A. sagrei* in their average levels of interspecific aggression. If allopatric individuals are more aggressive and less submissive when presented with a heterospecific intruder, then the submissive behavior of *A. carolinensis* in sympatric populations, such as those investigated in our study, may be adaptive (Peiman and Robinson 2010, Losin 2012). But because interspecific aggression can evolve as a byproduct of adaptive changes in intraspecific aggression (Case and Gilpin 1974), the evolution of interspecific signaling, aggression, and dominance hierarchies cannot be understood without considering the costs and benefits of both intra- and interspecific encounters (Mikami and Kawata 2004; Ord et al. 2011). These costs and benefits depend on ecological factors that can vary dramatically across space and time, such as population density and resource availability (reviewed in Grether et al. 2013).

Given the dearth of physical combat observed in our study, the potential costs of asymmetric interference competition for *A. carolinensis* are mostly indirect and take the form of displacement from foraging locations near the ground (Kamath et al. 2013). *Anolis carolinensis* and *A. sagrei* overwhelmingly recognize each other as different (interspecific mating events are very rare and no hybrid offspring have ever been identified [Losos 2009]), meaning that while they probably compete for

access to food, they do not compete for mates. Because suitable arthropod prey can be found both on the ground and in the foliage (Campbell 2000, Turnbough 2016), it is perhaps unsurprising that interspecific encounters on these islands seldom escalate to combat, which can carry large costs in the form of injury and wasted energy. However, the two attacks initiated by *A. sagrei* in our study suggest that this species' frequent interspecific displays are not always empty threats. If engaging in aggressive encounters with *A. sagrei* were not costly for *A. carolinensis*, we might expect that all else equal, *A. carolinensis* would eventually adapt by retreating from *A. sagrei* less often, even if interspecific differences in display frequency persist (Grether et al. 2013). This prediction deserves future testing.

Interspecific aggression and interference competition are common in nature (Schoener 1983, Peiman and Robinson 2010), but among anoles, a genus of over 400 species with numerous examples of interspecific habitat partitioning (Losos 2009), published accounts of interspecific behavioral interference and its consequences are rare. Furthermore, these accounts are mostly limited to species pairs that are extremely similar in morphology and behavior (i.e. belonging to the same ecomorph class; Jenssen et al. 1984, Hess and Losos 1991, Losin 2012) and scenarios in which at least one species is considered invasive (Losin 2012, Dufour et al. 2018, this study; but see Leal et al. 1998). We have provided thorough, systematically collected evidence for direct interference between anoles belonging to distinct ecomorph classes, suggesting two possible scenarios: 1) direct interference among different ecomorphs is rare overall and most likely to occur when species have only recently come in contact (i.e. one species is introduced), particularly when the resident species is less specialized in its habitat use prior to the introduction; 2) direct interference among different ecomorphs is more common than previously acknowledged, even in communities that have not experienced recent species introductions.

The perceived importance of interference competition in structuring communities is highly dependent on how interference is defined and measured (Peiman and Robinson 2010, Grether et al.

2017). Our work suggests that we should not overlook the potential for direct interference more subtle than frequent outright combat to mediate interspecific niche partitioning.

1.6 Acknowledgments

This work would not have been possible without the logistical and intellectual support provided by Irene Arpayoglou and staff at the Florida Department of Environmental Protection's Aquatic Preserve Program. We thank Carol Herzog, Dylan Gavagni, and staff at the St. Sebastian River Preserve for providing lodging. We also thank Jonathan Losos, Ambika Kamath, and Elizabeth Wolkovich for providing helpful feedback on the manuscript.

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Chapter 2

Character displacement in the midst of background evolution in island populations of *Anolis* lizards: a spatiotemporal perspective

This chapter is published and should be cited as follows:

Kamath, A., Herrmann, N. C., Gotanda, K. M., Shim, K. C., LaFond, J., Cottone, G., Falkner, H, Campbell, T.S., & Stuart, Y. E. (2020). Character displacement in the midst of background evolution in island populations of *Anolis* lizards: A spatiotemporal perspective. *Evolution*, 74(10), 2250-2264.

Associated data and R script available at [datadryad.org \(10.5061/dryad.pzgmsbcj0\)](https://datadryad.org/10.5061/dryad.pzgmsbcj0).

2.1 Summary

Negative interactions between species can generate divergent selection that causes character displacement. However, other processes cause similar divergence. We use spatial and temporal replication of island populations of *Anolis* lizards to assess the importance of negative interactions in driving trait shifts. Previous work showed that the establishment of *Anolis sagrei* on islands drove resident *Anolis carolinensis* to perch higher and evolve larger toepads. To further test the interaction's causality and predictability, we resurveyed a subset of islands nine years later. *Anolis sagrei* had established on one island between surveys. We found that *A. carolinensis* on this island now perch higher and have larger toepads. However, toepad morphology change on this island was not distinct from shifts on six other islands whose *Anolis* community composition had not changed. Thus, the presence of *A. sagrei* only partly explains *A. carolinensis* trait variation across space and time. We also found that *A. carolinensis* on islands with previously established *A. sagrei* now perch higher than a

decade ago, and that current *A. carolinensis* perch height is correlated with *A. sagrei* density. Our results suggest that character displacement likely interacts with other evolutionary processes in this system, and that temporal data are key to detecting such interactions.

2.2 Introduction

Understanding the frequency with which interspecific interactions lead to repeatable patterns of diversification helps us understand the processes shaping variation in nature. Character displacement theory, for example, suggests that negative interactions between ecologically similar species generate divergent natural selection that can drive evolutionary change (reviewed in Pfennig and Pfennig 2012). Such divergence is thought to play a major role in niche partitioning, coexistence, community assembly, and adaptive radiation (reviewed in Schluter 2000, Pfennig and Pfennig 2012).

However, character displacement theory is difficult to test in the field (Stuart and Losos 2013, Germain et al. 2018). Models suggest that as negative interspecific interactions drive trait divergence, the intensity of said interactions will attenuate relatively rapidly, making them hard to detect (Connell 1980, Schluter 2000). As such, researchers typically use present patterns of divergence to infer how past interactions shaped past selection and past evolution. Such inference is often uncertain (Simberloff and Boecklen 1981, Stuart and Losos 2013) because similar divergence patterns can arise from many different processes (Stuart et al. 2017).

One approach to inferring process from pattern is to monitor novel interactions between ecologically similar species *through time* and test for whether and how character displacement unfolds. A model case comes from a colonization event that caused new interactions between two seed-eating Galápagos finch species (Grant and Grant 2006). In 1984, the large ground finch (*Geospiza magnirostris*) arrived on the island of Daphne Major, encountering a long-established population of the medium ground finch (*Geospiza fortis*). Following a severe drought and the consequent decline in seed

abundance, the two species experienced increased competition for seeds and diverged in a key seed-use trait—beak size (Grant and Grant 2006).

The temporal span of that study—thirty years of pre- and post-interaction data for a single population of *G. fortis*—built a solid case for predictable, competition-driven character displacement on Daphne Major. Nevertheless, context mattered, as divergence in this system was contingent on more than just the presence of potential competitors. That is, observed patterns of stasis and change in beak size suggested that the strength of competition itself (and therefore the source of divergent selection) was controlled by the weather cycles that influence seed resources (Grant et al. 2017)—weather determined whether character displacement occurred (see Figure 2 in (Grant and Grant 2006)).

A second, more common way to make inferences about process from character displacement patterns is by comparing multiple populations within a focal taxon. Repeated character displacement *across space* can constitute strong evidence for competition-driven evolutionary divergence. For example, character displacement between sympatric interactors has been documented at multiple locations repeatedly and independently for several taxa, including stickleback (*e.g.*, Schluter and McPhail 1992), spadefoot toads (*e.g.*, Rice et al. 2009), and salamanders (*e.g.*, Adams 2010).

Spatial replication, as exemplified in comparative studies across populations, and temporal replication, as exemplified in long-term studies of single populations, can each help us understand the relative importance of character displacement amidst environmental contingencies and background evolution. However, these two approaches are more powerful when combined.

In a study taking advantage of the spatial replication offered by repeated species introductions to island populations, Stuart et al. (2014) examined habitat-use shifts and evolutionary change in one species of *Anolis* lizard following the arrival and establishment of a second species of anole. For millions of years, *Anolis carolinensis* was the only anole found in the southeastern United States as until recently, there were no other extant anoles. *Anolis sagrei* arrived in southern Florida in the late 1800s, was locally

abundant by the late 1940s (Collette 1961), and has since spread through Florida and beyond (Campbell and Echternacht 2003). The two species are similar enough in habitat use and diet that they are expected to compete for resources (Collette 1961, Campbell 2000). In Mosquito Lagoon, Florida, Stuart et al. (2014) compared five, hectare-sized islands with only *A. carolinensis* to six similar islands where *A. sagrei* had established sympatric populations sometime between 1995 and 2010 (Campbell 2000). They found that on every island with *A. sagrei*, *A. carolinensis* perched higher. Moreover, on average, those *A. carolinensis* populations co-occurring with *A. sagrei* had larger toepads with a larger number of specialized, clingy scales called lamellae. A common garden study revealed that toepad variation had a heritable component, and a variety of other potential causes for this repeated evolution, including environmental differences and non-random migration, were ruled out (Stuart et al. 2014). Because arboreality across the ~400 species of anoles is associated with larger toepads that have more lamellae (Glossip and Losos 1997, Macrini et al. 2003), and because toepad area correlates positively with clinging ability (Elstrott and Irschick 2004), Stuart et al. (2014) concluded that *A. carolinensis* repeatedly adapted to a more arboreal lifestyle in no more than ~20 generations following the introduction of a congener.

Notably, however, the six islands with both *A. carolinensis* and *A. sagrei* (where *A. carolinensis* perched the highest) were not always the islands with the largest toepad area or lamella number (Stuart et al. 2014). That is, island by island, morphological character displacement in *A. carolinensis* was less consistent than the habitat shift induced by the presence of *A. sagrei*. This motivates further investigation of the magnitude and direction of morphological evolution that is facilitated by the behavioral response of *A. carolinensis* to *A. sagrei*.

In this paper, we add a temporal component to Stuart et al. (2014) by revisiting the islands of Mosquito Lagoon to test predictions about the repeatability of behavioral shifts and morphological character displacement across both space and time (Table 2.1). We report new data, collected in 2019,

for *A. carolinensis* perch height and toepad morphology from six islands: three that had both *A. carolinensis* and *A. sagrei* in 2010 and still do ('two-species' islands); and, three that had only *A. carolinensis* in 2010 and 2019 ('one-species' islands). We compare these 2019 data to the data that were collected in 2010 (Stuart et al. 2014) to ask whether and how perch height and toepad traits changed through time on these islands (Question 1 in Table 2.1). These islands, whose species status did not change from 2010 to 2019 serve as a baseline and reveal whether character displacement is still evolving in this system, or whether *A. carolinensis* reached a stable adaptive optimum by 2010, in ~20 generations (Stuart et al. 2014).

We then report new data on perch height and toepad morphology from one island that had only *A. carolinensis* in 2010 but both species in 2019. We compare *A. carolinensis* perch height and toepad morphology in this single population before and after *A. sagrei* arrival (Question 2 in Table 2.1). We predicted that *A. carolinensis* on this island would perch higher and have larger toepads with more lamellae than they did prior to *A. sagrei* arrival. This comparison of change in toepad traits provides a complementary test of the conclusions previously drawn from comparative data (Stuart et al. 2014): that novel interactions with *A. sagrei* result in toepad divergence.

Finally, to better understand how variation in interspecific interactions might lead to observed variation in the magnitude of character displacement in this system, we quantify finer-scale effects of *A. sagrei* presence on *A. carolinensis* perch height in two ways. First, we test whether average *A. carolinensis* perch heights correlate positively with *A. sagrei* population density (Question 3a). If yes, this suggests that variable character displacement across islands might depend in part on island-to-island variation in *A. sagrei* population dynamics. Second, *A. sagrei* density could affect *A. carolinensis* perch heights through different types of negative interactions, e.g., resource competition, interference competition, apparent competition, or intraguild predation (Schluter 2000). Testing among these is difficult. Some evidence suggests that interference competition is important in this *Anolis* system

(Edwards and Lailvaux 2013, Culbertson and Herrmann 2019). In particular, *A. carolinensis* are substantially more likely than *A. sagrei* to flee from interspecific interactions, with males retreating upward more often than expected by chance (Culbertson and Herrmann 2019). Thus, we predicted that among *A. carolinensis* on two-species islands, individuals observed in the immediate vicinity of *A. sagrei* would perch higher than individuals observed with no *A. sagrei* nearby (Question 3b). This finding would further implicate agonistic, interference interactions in the perch height shift.

Table 2.1. Study questions.

Question 1	Has <i>A. carolinensis</i> perch height and toepad morphology shifted on islands whose anole communities did not change between 2010 and 2019?
Question 2	Has <i>A. carolinensis</i> perch height and toepad morphology shifted on one island with a recent <i>A. sagrei</i> arrival? <i>Prediction:</i> On the island with recent <i>A. sagrei</i> arrival, <i>A. carolinensis</i> would perch higher and have larger toepads with more lamellae than they did prior to <i>A. sagrei</i> arrival.
Question 3a	Does variation in the island-wide density of <i>A. sagrei</i> explain population-level variation in <i>A. carolinensis</i> perch height across islands? <i>Prediction:</i> Islands with higher density of <i>A. sagrei</i> would have higher mean perch heights for <i>A. carolinensis</i> .
Question 3b	Does variation in the local presence of <i>A. sagrei</i> explain variation among individuals in <i>A. carolinensis</i> perch height within islands? <i>Prediction:</i> Among <i>Anolis carolinensis</i> on two-species islands, individuals would perch higher when individual <i>A. sagrei</i> were observed nearby.

2.3 Methods

We studied seven islands in 2019 that were also studied in 2010 (Table 2.2). *Anolis carolinensis*, the focal species, was present on all seven islands in 2010 and 2019 (Stuart et al. 2014, this study). *Anolis sagrei* was present on three of the study islands in both 2010 and 2019 (Channel, North Twin, and Yang). *A. sagrei* was absent on three islands in both 2010 and 2019 (Hornet, Crescent, and Osprey). These six islands are referred to in this manuscript as ‘control’ islands, for brevity, because their species category (i.e., one- versus two-species) did not change from 2010 to 2019. One island, South Twin, was a

one-species island in 2010 and a two-species island in 2019. *Anolis sagrei* arrived on South Twin sometime between 2010 and 2018, per island surveys by Y.E.S., T.S.C., and K.C.S. on July 7, 2018.

Table 2.2 *Anolis sagrei* presence status, *A. carolinensis* perch height sample size, and *A. carolinensis* morphology sample size by island for 2010 and 2019. For sample sizes, males (m) are listed before the “/” and females (f) after. South Twin, which was a one-species island in 2010 and a two-species island in 2019, is indicated in bold.

Island	Code	Two-species?		Perch height sample size (m/f)		Morphology sample size (m/f)	
		2010	2019	2010	2019	2010	2019
North Twin	ntw	Yes	Yes	48 / 21	45 / 26	33 / 11	30 / 18
Channel	cha	Yes	Yes	51 / 15	45 / 30	38 / 15	31 / 16
Yang	yan	Yes	Yes	57 / 14	35 / 16	41 / 16	31 / 12
South Twin	stw	No†	Yes	60 / 38	46 / 30	34 / 24	35 / 18
Osprey	osp	No	No	52 / 15	44 / 21	33 / 10	30 / 19
Crescent	cre	No	No	50 / 12	36 / 24	38 / 10	34 / 23
Hornet	hor	No	No‡	60 / 27	32 / 23	44 / 15	30 / 24

† A single, male *A. sagrei* was observed on South Twin in 2010 (Y.E.S. personal observation), suggesting that colonization had already started. That individual was captured and euthanized. No *A. sagrei* were observed on South Twin in 2011.

‡ A single, male *A. sagrei* was observed on Hornet Island in 2019. It was captured on the westernmost edge of the island (the closest point to the mainland) and euthanized.

From May 29 to June 14, 2019, we visited each of the seven islands on multiple days. One to five workers landed on an island by about 7:00 am and stayed until about 12:30 pm. We walked through the habitat until an undisturbed *A. carolinensis* individual was observed. We noted the lizard’s perch and attempted to capture it by hand or with lasso poles. We recorded perch height (using tape measures) and sex for each lizard. Sexes were distinguished based on body size and shape, including dewlap characteristics, as well as the presence of externally visible hemipenes and enlarged post-anal scales in males that were captured. We transported captured lizards to field housing for toepad data collection. After measuring toepads, we numbered each lizard with permanent ink to avoid repeated measures of the same individual and released it where captured, typically within 30 hours.

In field housing, we anesthetized lizards using isoflurane. While the lizard was anesthetized, we used digital calipers to measure snout-vent length (SVL) to the nearest mm as a measure of body size.

We then used a digital scanner at 2400dpi to image the fourth (longest) toe of each hind foot, following (Glossip and Losos 1997, Stuart et al. 2014).

We used FIJI (Schindelin et al. 2012) and the plugin ObjectJ v1.04r (Vischer and Nastase 2018) to count lamellae and measure toepad area from the digital scans. Following Stuart et al. (2014), we counted the number of lamellae on the third and fourth (*i.e.*, distal-most) phalanges of each toe. We then traced the region encompassed by those lamellae to measure the area of the left and right toepad. Lamella counts and pad areas were averaged across sides. Y.E.S. conducted all phenotyping (as they did for the 2010 data), after practicing on a burn-in sample of 50 images. Information on source island was not attached to toepad photographs during phenotyping.

Histograms of lamella number and toepad area were normally distributed for both 2010 and 2019 data, though 2010 toepad area showed a heavy left tail. We ran linear regressions of toepad traits $\sim$ SVL x sex with females as the baseline to assess the need for size-correction prior to further analysis. In the 2019 data, average toepad area was positively related to SVL and the relationship varied by sex ($\beta_{\text{size}} = 0.09$, $\beta_{\text{male}} = -2.70$, $\beta_{\text{interaction}} = 0.06$, all $p < 0.0001$, Adj. $R^2_{\text{model}} = 0.88$). Average lamella number did not vary with SVL ($\beta_{\text{size}} = 0.05$, $\beta_{\text{male}} = 1.48$, $\beta_{\text{interaction}} = -0.01$, all $p > 0.19$, Adj. $R^2_{\text{model}} = 0.27$). In the 2010 data also, average toepad area was positively related to SVL and the relationship differed by sex ($\beta_{\text{size}} = 0.08$, $\beta_{\text{male}} = -2.76$, $\beta_{\text{interaction}} = 0.06$, all $p < 0.0003$, Adj. $R^2_{\text{model}} = 0.87$). Again, lamella number did not vary with SVL ($\beta_{\text{size}} = 0.06$, $\beta_{\text{male}} = 1.61$, $\beta_{\text{interaction}} = -0.01$, all $p > 0.18$, Adj. $R^2_{\text{model}} = 0.27$). Thus, we corrected toepad area but not lamella number for SVL.

We size-corrected toepad area separately for males and females, due to the significant interaction between sex and SVL in the regression against toepad area. Size correction used: $M_{s,i} = M_{0,i} * (L_s / L_{0,i})^b$, where $M_{s,i}$ is the size-corrected toepad area for individual i , $M_{0,i}$ is the non-size-corrected toepad area for individual i , L_s is the overall mean for SVL across all individuals of the given sex, and $L_{0,i}$ is the SVL of individual i . b is the common within-group slope calculated from a linear mixed model of the

log of the individual toepad area ($\log_{10}(M_{0,i})$) regressed on the log of the individual SVL ($\log_{10}(L_{0,i})$) (Lleonart et al. 2000, Oke et al. 2016). In this regression, we included year as a fixed effect and island as a random effect. This mixed model was run using the *lmer* function (in the *lme4* package in R; Bates et al. 2014), coded as follows: $\text{toepad area} \sim \text{SVL} + \text{year} + (1 | \text{island})$. *b* for females and males was 1.37 (s.e. = 0.12) and 1.97 (s.e. = 0.06), respectively.

Data Analysis

To investigate whether *A. carolinensis* on the six control islands (three one-species and three two-species islands) changed their perch heights, toepad area, and lamella number from 2010 to 2019 (Question 1), we built a linear mixed effects model and combined data from 2010 (Stuart et al. 2014) and 2019 (this study). Our statistical null hypothesis was that we would find no change in *A. carolinensis* perch height or morphology because there had been no changes in the presence of *A. sagrei*. This effectively posits that *A. carolinensis* trait shifts in response to *A. sagrei* had stabilized by 2010. Perch height, size-corrected toepad area, and lamella number were response variables, with each modeled separately. Fixed effects were year, species category (one- or two-species), a year x species category interaction, and sex. Island was included as a random effect. We used *lme* in the R package *nlme* (Pinheiro et al. 2014) coding models as follows: $\text{response} \sim \text{year} \times \text{category} + \text{sex}$, $\text{random} = \sim 1 | \text{island}$. Here, the year effect evaluates Question 1 by revealing whether these populations changed from 2010 to 2019; the year x species category effect tests whether changes with time differed between one- and two-species islands.

To compare habitat use and morphology by *A. carolinensis* on South Twin in 2019 versus 2010 (Question 2), we regressed perch height, size-corrected toepad area, and lamella number (with each modeled separately) against year and sex. We used *lm* in R's *stats* package, coded as follows: $\text{response} \sim \text{year} + \text{sex}$. A positive, significant effect of year suggests an increase in 2019 relative to 2010.

We further tested Question 2 using models that pooled all islands. These models tested whether change observed on South Twin was significantly different from change observed on the six control islands. Again using *lm*, we regressed perch height, size-corrected toepad area, and lamella number, in turn, against year, island, a year x island interaction, and sex. We built the model so that South Twin females from 2010 would be the baseline comparison group. In this way, a significant year effect suggests that all else equal, lizards on South Twin have a different trait mean in 2019 than in 2010. A significant island effect means that a given island has a different base trait value than South Twin. A significant year x island effect means that any change from 2010 to 2019 on that island differed from temporal change observed on South Twin.

We next asked whether *A. carolinensis* perch height depends on the population density of *A. sagrei* (Question 3a). In 2019, we estimated the relative density of *A. sagrei* across islands using observation-per-unit-time surveys. One researcher (G.C.) walked each two-species island twice, including South Twin, conducting an hour-long survey for *A. sagrei* between 7:15 and 9:00 am. The average of these two survey counts is a proxy for island-wide density. We regressed, using *lm*, island mean perch height against island mean *A. sagrei* count.

Previous studies showed that the presence of *A. sagrei* causes an increase in *A. carolinensis* perch height (Campbell 2000, Stuart et al. 2014, Pringle et al. 2019). If this is partly due to an agonistic interaction (Edwards and Lailvaux 2013, Culbertson and Herrmann 2019), we expect that individual *A. carolinensis* on two-species islands should perch higher when *A. sagrei* is nearby (Question 3b). In both 2010 (Stuart et al. 2014) and 2019, for every observed *A. carolinensis* perch height, we noted whether any *A. sagrei* individuals were within a ~1m-radius cylinder, centered at the observed perch site and stretching from ground to sky. We used a linear mixed model to regress *A. carolinensis* perch height against the presence or absence of *A. sagrei* near the perch with *A. carolinensis* sex as a fixed effect. Island was included as a random effect. As above, we used *lme*, coding the model as follows: perch

height ~ sagrei presence + sex, random = ~1|island. We ran separate regressions for 2010 and 2019 data because South Twin was a one-species island in 2010 and so replicate numbers differ from year to year.

2.4 Results

Question 1

Perch height: For control islands, *i.e.*, islands whose species category (one-species or two-species) did not change between 2010 and 2019, a linear mixed model detected a significant interaction between year and species category. Compared to one-species islands, two-species islands with *A. sagrei* showed significant increases in *A. carolinensis* perch heights from 2010 to 2019 (Table 2.3, Figure 2.1).

Table 2.3 Change in *A. carolinensis* perch heights on one-species and two-species control islands from 2010 to 2019. Results from a linear mixed effects model: perch height ~ year x one-versus-two species + sex + (1|island). Here, females from one-species islands in 2010 are the baseline (*i.e.*, the intercept) against which all other categories are compared.

	β (cm)	Std. Err.	D.F.	t-value	p-value
Perch Height Intercept	87.7	11.7	786	7.5	< 0.001
Year (2019)	4.1	8.9	786	0.5	0.643
Two-species (Yes)	66.7	15.0	4	4.5	0.011
Sex (Male)	27.4	6.8	786	4.0	< 0.001
Year x two-species	57.6	12.4	786	4.6	< 0.001

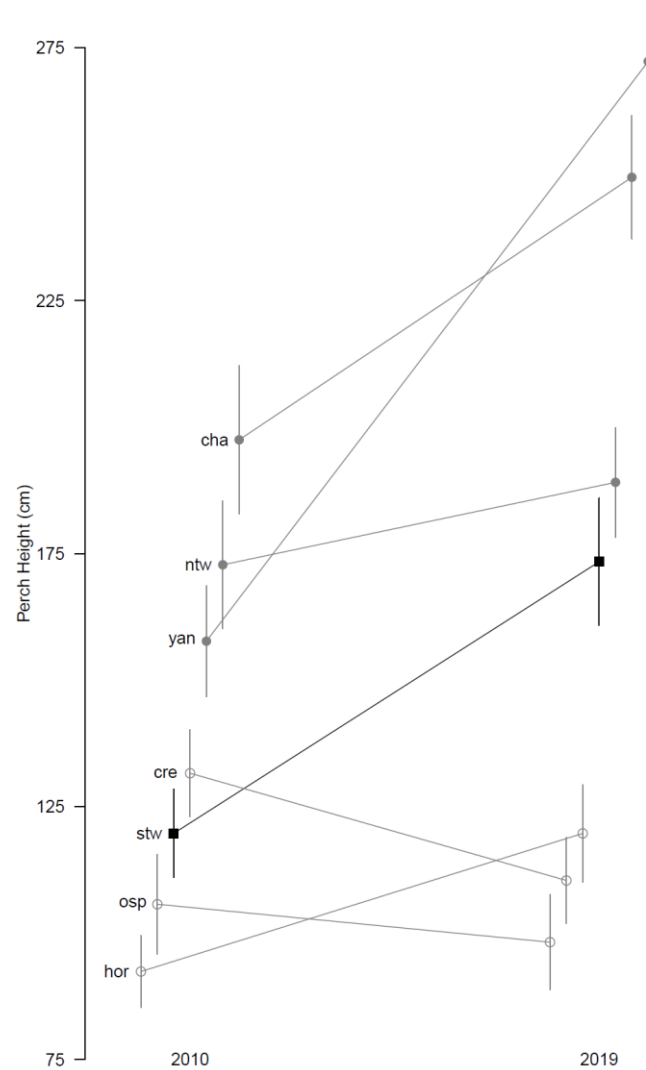


Figure 2.1 Mean perch heights for *A. carolinensis*, by island, in 2010 and 2019. Standard errors are shown. Islands are staggered within year. Control islands are in grey. Filled circles are two-species islands. Open circles are one-species islands. The black square is South Twin. Recall that South Twin was a one-species island in 2010, and a two-species island in 2019.

Toepad area: For control islands, a linear mixed model found no year effect and no year by species category interaction for toepad area (Table 2.4; Figure 2.2). The difference in toepad area between islands with and without *A. sagrei* was in the same direction as observed in Stuart et al. (2014), though the difference detected here using a smaller sample of islands was not significant ($p = 0.121$).

Table 2.4 Change in *A. carolinensis* size-corrected toepad area on one-species and two-species control islands from 2010 to 2019. Results from a linear mixed effects model: toepad area ~ year x species category + sex + (1|island). Here, females from one-species islands in 2010 are the baseline (*i.e.*, the intercept) against which all other categories are compared.

	β	Std. Err.	D.F.	t-value	p-value
Intercept	2.52	0.08	593	32.2	<0.001
Year (2019)	0.04	0.03	593	1.3	0.207
Two-species (Yes)	0.21	0.11	4	2.0	0.121
Sex (Male)	1.56	0.02	593	61.6	<0.001
Year x two-species	0.04	0.05	593	1.0	0.327

Lamella number: For control islands, lamella number did not change between 2010 and 2019, and we observed no year by species category interaction (Table 2.5, Figure 2.2). The difference in lamella number between islands with and without *A. sagrei* was in the same direction as observed in Stuart et al. (2014), though the difference detected here using a smaller sample of islands was not significant ($p = 0.154$).

Table 2.5. Change in *A. carolinensis* lamella number on two-species and one-species control islands from 2010 to 2019. Results from a linear mixed effects model: lamella number ~ year x one-versus-two species + sex + (1|island). Here, females from one-species islands in 2010 are the baseline (*i.e.*, the intercept) against which all other categories are compared.

	β	Std. Err.	D.F.	t-value	p-value
Intercept	22.70	0.21	593	107.8	<0.001
Year (2019)	0.11	0.11	593	0.97	0.334
Two-species (Yes)	0.49	0.28	4	1.76	0.154
Sex (Male)	1.29	0.09	593	14.55	<0.001
Year x two-species	-0.22	0.16	593	-1.38	0.168

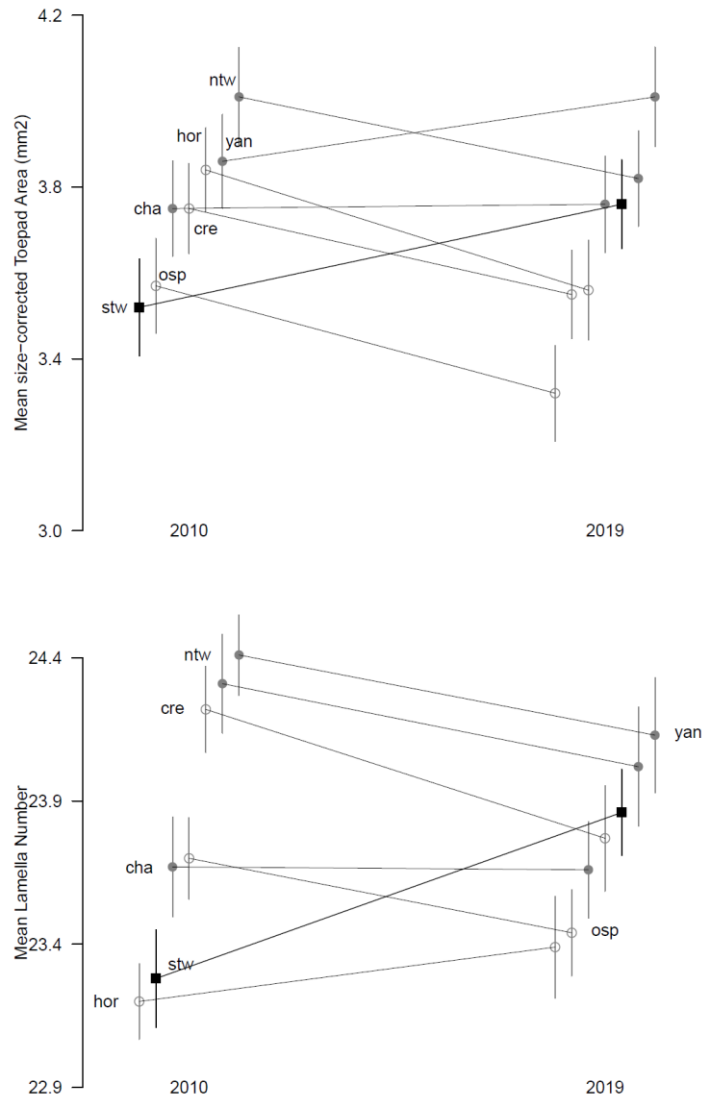


Figure 2.2 Change from 2010 to 2019 in mean size-corrected toepad area and mean lamella number, by island. Standard errors shown. Lines connect the same island across years. These are raw values; they do not take into account the sex and year x island effects reported in Tables 2.7 and 2.8. Control islands are in grey. Filled circles are two-species islands. Open circles are one-species islands. The black square is South Twin.

Question 2

Linear models for South Twin only

(i) Perch Height: A linear model with just lizards from South Twin showed that *Anolis carolinensis* on

South Twin perched 54cm higher in 2019 compared to 2010 ($p = 0.0002$; $mean^{+1se}_{-1se}$, $119.7^{128.4}_{111.0}$ cm to

173.4^{186.0}_{160.8} cm). The same model showed that males perched higher than females by 49cm, across years, all else equal ($p = 0.0011$).

(ii) Toepad Area: As predicted, size-corrected toepad area for *A. carolinensis* increased on South Twin from 2010 to 2019 ($mean_{-1se}^{+1se}$; 3.52^{3.63}_{3.40} mm² to 3.76^{3.86}_{3.65} mm²), an increase of approximately 7%. Linear regression with year and sex as predictors, and 2010 females as the baseline, revealed a positive, significant effect of 2019 versus 2010 ($\beta_{2019} = 0.12$, $p = 0.028$). Males had toepads with significantly larger areas ($\beta_{male} = 1.55$, $p < 0.001$).

(iii) Lamella number: Although mean lamella number for *A. carolinensis* was higher on South Twin in 2019 relative to 2010 ($mean_{-1se}^{+1se}$; 23.28^{23.45}_{23.11} lamellae to 23.77^{23.96}_{23.59} lamellae), an increase of approximately 2%, though the increase was not significantly different from zero ($\beta_{2019} = 0.37$, $p = 0.079$). Males had toepads with significantly more lamellae than females ($\beta_{male} = 1.52$, $p < 0.001$).

Is change on South Twin between 2010 and 2019 significantly different from change on control islands?

(i) Perch Height: We used a linear model with all islands to ask whether perch height change on South Twin was different from changes on control islands whose species number did not change between 2010 and 2019. We structured the model so that South Twin served as the baseline against which other islands were compared. The year effect was significant ($p < 0.001$), again showing that *A. carolinensis* perch height increased on South Twin all else equal (by 53.9cm, Table 2.6). Year x island interactions revealed significantly different perch height shifts by *A. carolinensis* on four other islands compared to South Twin (Table 2.6). Overall, *A. carolinensis* on one-species islands showed either an increase (Hornet) or a decrease (Osprey and Crescent) in perch height from 2010 to 2019, relative to South Twin. On two-species islands, *A. carolinensis* on Yang Island increased more than South Twin. The year x island interaction was not significant for Channel or North Twin, suggesting that these islands increased their perch height similarly to South Twin (Table 2.6). Summing the coefficient of the year effect with the

island specific coefficient for the year x island interaction gives the model's best estimates for 2010 to 2019 change on each island (final column, Table 2.6). The rank order of perch height change from positive to *negative* was: Yang, Channel, South Twin, Hornet, North Twin, *Osprey*, and *Crescent* (Table 2.6).

Table 2.6 *A. carolinensis* perch heights changed from 2010 to 2019 on five islands. Results from a linear model: perch height ~ year x island + sex. Adding the coefficient for the effect of 2019 to the island x year interaction coefficient gives the estimated change in perch height from 2010 to 2019 for a given island (final column). Here, females from one-species islands in 2010 are the baseline (*i.e.*, the intercept) against which all other categories are compared.

	β (cm)	Std. Err.	t-value	p-value	Estimated within island change
Perch Height Intercept	100.3	9.6	10.4	<0.001	NA
Year (2019)	53.9	13.4	4.0	<0.001	53.9†
Sex (Male)	31.7	13.7	5.2	<0.001	NA
Channel Island (two species)	71.6	14.3	5.0	<0.001	58.5
2019 x Channel	4.6	20.2	0.2	0.82	
North Twin Isl. (two species)	50.4	13.8	3.6	<0.001	18.3
2019 x North Twin	-35.6	20.0	-1.8	0.075	
Yang Island (two species)	31.9	13.7	2.3	0.020	118.4
2019 x Yang	64.4	21.0	3.1	0.002	
Crescent Island (one species)	5.7	14.3	0.4	0.69	-14.6
2019 x Crescent	-68.5	20.8	-3.3	0.001	
Hornet Island (one species)	-29.8	12.9	-2.3	0.021	30.7
2019 x Hornet	-23.2	20.2	-1.1	0.25	
Osprey Island (one species)	19.2	13.9	-1.4	0.17	-4.4
2019 x Osprey	-58.3	20.3	-2.9	0.004	
Model: $F_{14, 954} = 26.7$, $p < 0.0001$, Adj. $R^2 = 0.27$					
† This is the estimate of the change from 2010 to 2019 on South Twin, all else equal.					

(ii) Toepad Area: For size-corrected toepad area, the effect of year was positive and significant ($p = 0.034$; Table 2.7), again showing that *A. carolinensis* toepad area increased on South Twin from 2010 to 2019. The year x island effects were predominantly negative, though none were significant, meaning the toepad area increase on South Twin was not statistically distinguishable from changes on any other

island. The rank order of toepad area change from positive to *negative* was: Yang, South Twin, Crescent, Channel, Hornet, North Twin, and *Osprey* (Table 2.7).

Table 2.7 Size-corrected toepad area increased on all islands in 2019, relative to 2010. South Twin females in 2010 are the baseline of this model. ‘Year x island’ change sums the coefficients of the year effect (0.11) and a specific interaction effect for an estimate of island change from 2010 to 2019. Here, females from one-species islands in 2010 are the baseline (*i.e.*, the intercept) against which all other categories are compared.

	β	Std. Err.	t-value	p-value	Estimated within island change
Intercept	2.61	0.039	65.85	<0.001	NA
Year (2019) †	0.11	0.054	2.12	0.034	0.11†
Channel Island (two species)	0.02	0.054	0.29	0.77	0.10
2019 x Channel	-0.01	0.078	-0.12	0.90	
North Twin Isl. (two species)	0.23	0.06	3.99	<0.001	0.00
2019 x North Twin	-0.11	0.08	-1.43	0.15	
Yang Island (two species)	0.12	0.05	2.32	0.020	0.15
2019 x Yang	0.03	0.08	0.45	0.65	
Crescent Island (one species)	-0.10	0.06	-1.79	0.074	0.11
2019 x Crescent	-0.01	0.08	-0.09	0.93	
Hornet Island (one species)	0.06	0.05	1.20	0.23	0.02
2019 x Hornet	-0.10	0.08	-1.27	0.20	
Osprey Island (one species)	-0.24	0.06	-4.22	<0.001	-0.01
2019 x Osprey	-0.12	0.08	-1.49	0.14	
Sex (Male)	1.56	0.02	68.07	<0.001	NA

Model: $F_{14, 697} = 352.5$, $p < 0.0001$, Adj. $R^2 = 0.87$

† This is the estimate of the change from 2010 to 2019 on South Twin, all else equal.

(iii) Lamella Number: For lamella number, the effect of year was positive and significant ($p = 0.046$; Table 8), showing that South Twin *A. carolinensis* had more lamellae in 2019 than in 2010. The year x island effects were predominantly negative, but significant on only one island (Yang; Table 2.8). Thus, our results suggest that the lamella count increase on South Twin was not statistically distinguishable from changes on other islands. The rank order of lamella number change from positive to *negative* was: Hornet, South Twin, Channel, *Crescent*, *Osprey*, *North Twin*, and *Yang* (Table 2.8).

Table 2.8 Lamella number increased on South Twin in 2019, relative to 2010. South Twin females in 2010 are the baseline of this model. ‘Year x island change’ sums the coefficients of the year effect (0.38) and interaction effect for an estimate of island specific change from 2010 to 2019. Here, females from one-species islands in 2010 are the baseline (*i.e.*, the intercept) against which all other categories are compared.

	β	Std. Err.	t-value	p-value	Estimated within island change
Intercept	22.51	0.14	158.96	<0.001	NA
Year (2019) †	0.38	0.192	1.99	0.046	0.38†
Channel Island (two species)	0.20	0.19	1.07	0.28	0.066
2019 x Channel	-0.32	0.28	-1.14	0.25	
North Twin Isl. (two species)	0.80	0.20	-1.59	<0.001	-0.120
2019 x North Twin	-0.50	0.28	-1.77	0.078	
Yang Island (two species)	0.94	0.19	5.00	<0.001	-0.286
2019 x Yang	-0.67	0.28	-2.40	0.017	
Crescent Island (one species)	0.66	0.20	3.31	0.001	-0.100
2019 x Crescent	-0.48	0.28	-1.75	0.080	
Hornet Island (one species)	-0.30	0.19	-1.59	0.11	0.494
2019 x Hornet	0.11	0.27	0.40	0.69	
Osprey Island (one species)	0.17	0.20	0.82	0.41	-0.104
2019 x Osprey	-0.49	0.28	-1.71	0.088	
Sex (Male)	1.33	0.08	16.26	<0.001	NA

Model: $F_{15, 696} = 24.6$, $p < 0.0001$, Adj. $R^2 = 0.33$

† This is the estimate of the change from 2010 to 2019 on South Twin, all else equal.

Question 3a.

Does variation in the island-wide density of A. sagrei explain population-level variation in A. carolinensis perch height across islands?

Average counts during hour-long surveys for *A. sagrei* in 2019 were 18.5 (South Twin), 32.5 (North Twin), 41.5 (Channel), and 43.0 (Yang). Mean *A. carolinensis* perch height was positively related to average *A. sagrei* count (Figure 2.3). For every additional *A. sagrei*, the mean perch height of *A. carolinensis* increased by 3.4cm ($p = 0.0002$). A regression including only the two-species islands from 2019 showed a similar effect with only four island means (3.8cm perch increase per additional *A. sagrei*) but was only significant at the 0.10 level ($p = 0.09$).

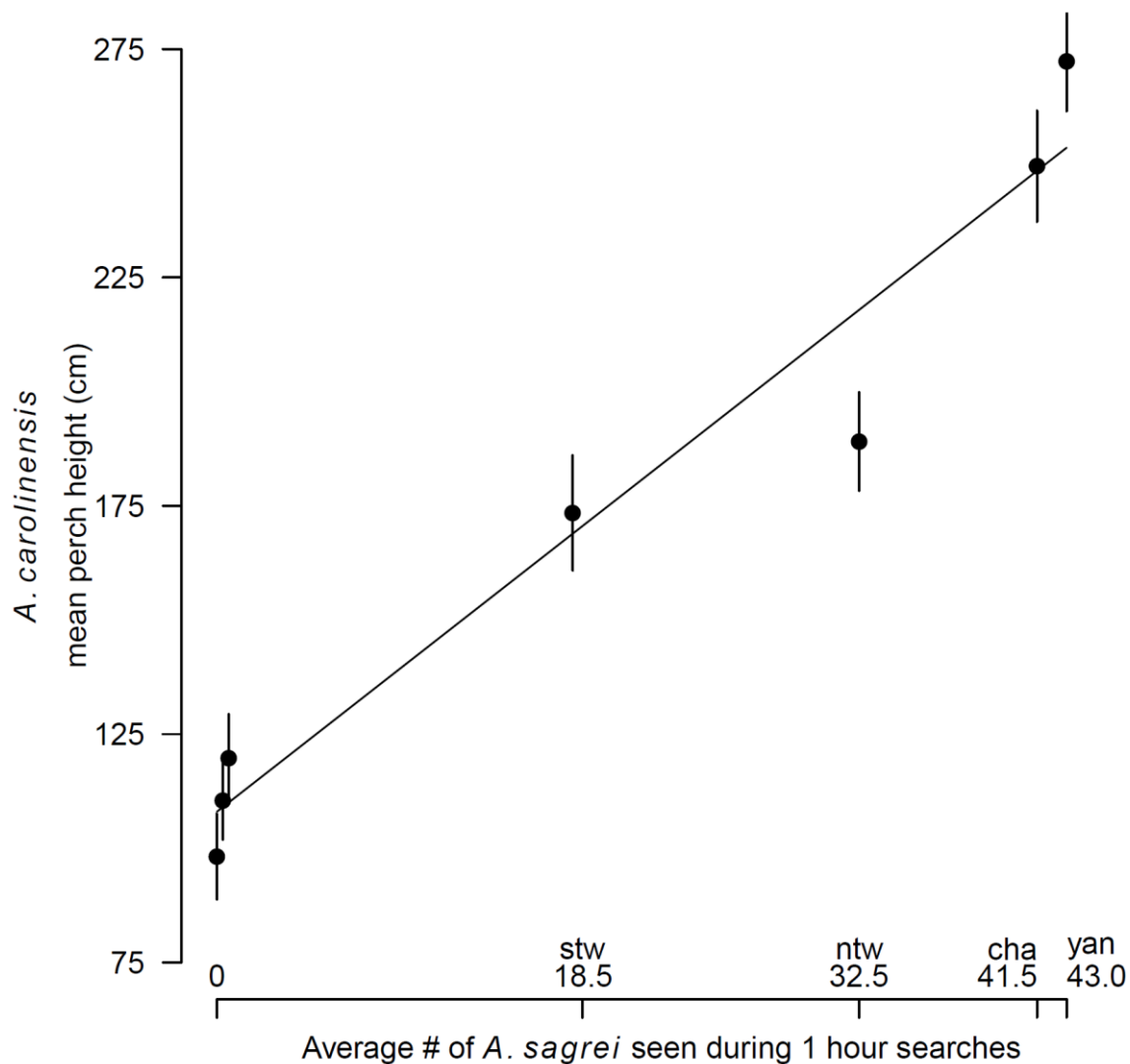


Figure 2.3 *A. carolinensis* perch height is positively correlated with mean *A. sagrei* density ($\beta = 3.4\text{cm}$, $p = 0.0002$). Excluding the one-species islands from the linear regression reveals a similar, positive relationship, but it is no longer significant ($\beta = 3.8\text{cm}$, $p = 0.08$). Island means are shown with standard errors. Values at $x = 0$ are jittered.

Question 3b.

Does variation in the local presence of A. sagrei explain individual-level variation in A. carolinensis perch height within islands?

In 2019, the presence of *A. sagrei* near an *A. carolinensis* perch was significantly correlated with a 55cm increase in *A. carolinensis* perch height ($p < 0.0001$; Table 2.9A; Figure 2.4A). Sex differences in perch

height disappeared in this model ($p = 0.51$), suggesting that male and female *A. carolinensis* are perching similarly once nearby *A. sagrei* are accounted for. The opposite result was found in 2010. *A. sagrei* nearby was negatively correlated with *A. carolinensis* perch height on two species islands ($\beta_{\text{nearby}} = -43\text{cm}$, $p = 0.01$; Table 2.9B), whereas being male was positively correlated ($\beta_{\text{male}} = 50\text{cm}$, $p = 0.004$; Table 9; Figure 2.4B).

Table 2.9 Nearby *A. sagrei* is correlated with *A. carolinensis* perch height. (A) Results for 2019 linear mixed model with island as a random effect. South Twin as the baseline. (B) Results for 2010 linear mixed model with island as a random effect. Channel is the baseline. South Twin was one-species in 2010.

	Coefficient	Std.	Deg.	t-	p-value
	(cm)	Err.	Freedom	value	
(A) 2019					
Intercept	186	21.1	261	8.8	< 0.001
<i>A. sagrei</i> nearby (Yes)	55	12.6	261	4.3	< 0.001
Sex (Male)	8.1	12.2	261	0.66	0.510
(B) 2010					
Intercept	147	16.9	196	8.6	< 0.001
<i>A. sagrei</i> nearby (Yes)	-43	17.1	196	-2.4	0.012
Sex (Male)	50	17.1	196	2.9	0.004

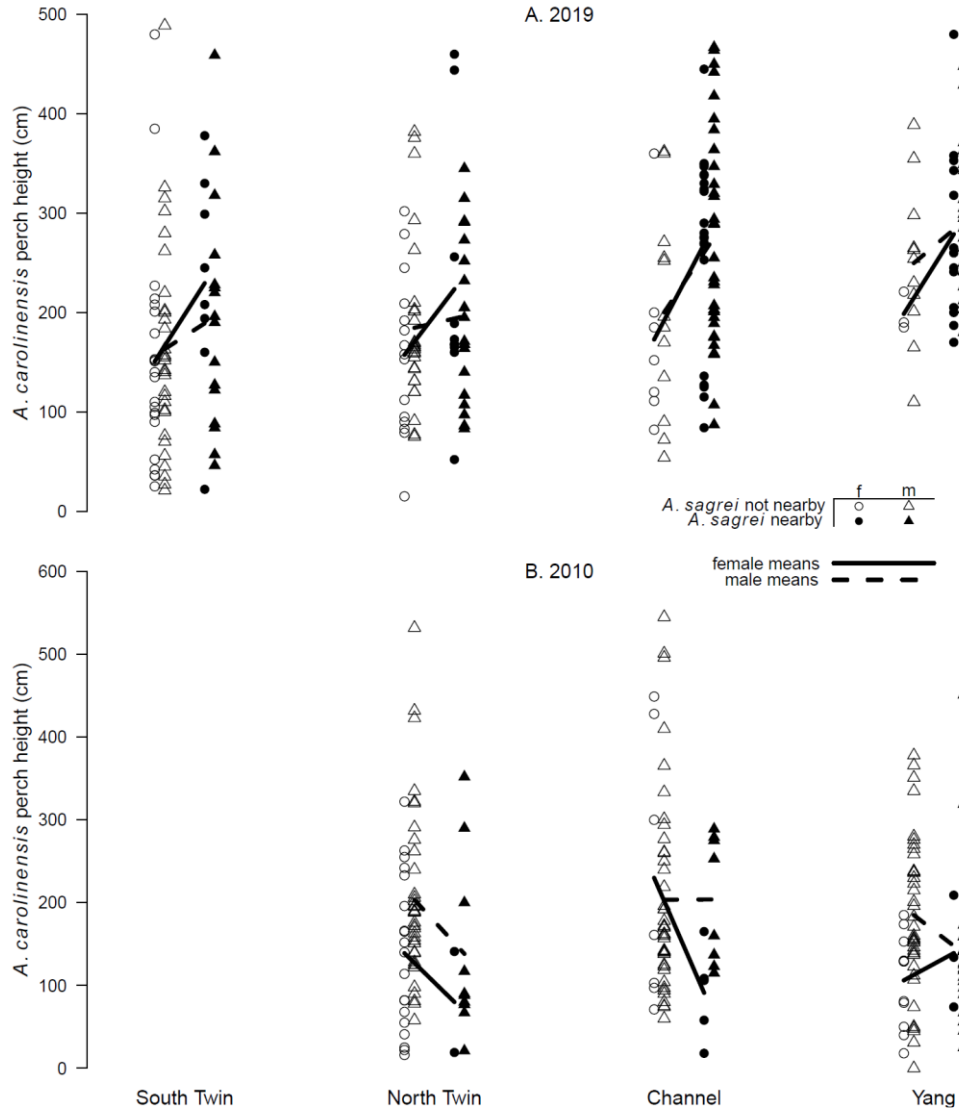


Figure 2.4 Finding *A. sagrei* nearby is correlated with a significant increase in perch height by *A. carolinensis* in 2019 (panel A; Table 2.9A) but not 2010 (panel B; Table 2.9B). Each point is an individual. Males are offset from females. Solid lines connect female means in each *sagrei*-nearby category. Dotted lines connect male means. South Twin has no data in 2010 because it was an *A. carolinensis*-only island at that time.

2.5 Discussion

Species introductions can establish replicated competitive arenas that reveal the frequency and repeatability of character displacement (Stuart and Losos 2013). A drawback, however, to such natural experiments is that pre-introduction information is often lacking. Instead, allopatric populations are used as proxies for an ancestral state and so the reliability of inference depends on the reliability of the proxy. Long term datasets can provide pre-introduction data and thereby improve inference because a given population serves as its own baseline (e.g., Grant and Grant 2006). In this study, we added a

temporal component to a study of character displacement that previously documented divergence spatially, across island replicates at a single point in time. Sampling nine years after that study reveals that the coarse pattern of repeated character displacement observed in this system remains. This is particularly true for the behavioral perch height response of *A. carolinensis* to *A. sagrei*, which remained large and largely predictable at both the across-island and within-island levels. However, morphological evolution of toepads is not linked as strongly as predicted to the observed behavioral change, indicating that the process of character displacement is nuanced, dynamic, and requires investigation across both space and time to contextualize it amidst background evolution.

Perch height change

In agreement with prior results (Stuart et al. 2014), we found that *A. sagrei* presence is a significant predictor of *A. carolinensis* perch height. On average, in 2019, *A. carolinensis* perched higher when sympatric with *A. sagrei*. This was true on islands whose species category (one versus two species) did not change between 2010 and 2019 (addressing Question 1), and on South Twin, which was a two-species island in 2019 but not 2010 (addressing Question 2). Together, these results corroborate experimental and comparative evidence that *A. sagrei* presence is the cause of habitat-use shifts in *A. carolinensis* (Stuart et al. 2014, Pringle et al. 2019). Behavioral plasticity is most likely responsible for initial shifts in perch height. Individual *A. carolinensis* alter their habitat use in real-time when an *A. sagrei* individual is introduced nearby (Culbertson and Herrmann 2019), and introduction experiments showed detectable, population-level shifts within weeks (Campbell 2000, Stuart et al. 2014). However, we cannot rule out an evolved component to this behavioral shift, especially as it persists across generations.

Our temporal approach further reveals that shifts in *A. carolinensis* perch height are not one-time events that stabilize shortly after *A. sagrei* arrival. We found that *A. carolinensis* on two-species islands perched higher in 2019 than they did in sympatry in 2010. That this increase did not occur on one-species islands again implicates *A. sagrei* as the cause and suggests that the intensity of the interspecific interaction has magnified over time.

Change in morphology

The establishment of *A. sagrei* on South Twin after the resident *A. carolinensis* population had been studied in 2010 allowed us to test the extent to which morphological character displacement in this system is predictable (Question 2). Comparing *A. carolinensis* on South Twin in 2010 and 2019, we found

that toepad area was significantly higher in 2019 than in 2010, and there was a trend toward more lamellae in 2019 ($p = 0.079$), despite sampling fewer islands than Stuart et al. (2014). Had we restricted our 2019 sampling to this single island, we would have concluded that toepad evolution is predictable in this system. There are three ways, however, in which additional results from this study complicate our prior understanding of morphological character displacement in this system (Stuart et al. 2014).

First, the toepad change observed on South Twin from 2010 to 2019 was statistically indistinguishable from the observed change on both one- and two-species islands, where zero change was expected (Table 2.7, Table 2.8). Thus, despite some evidence for adaptive morphological evolution arising due to a novel negative interaction, that signal does not stand out against background evolution in control populations.

Second, we detected no significant differences in toepad morphology between *A. carolinensis* on two-species and one-species control islands (Question 1, Table 2.4 and 2.5). That is, the morphological pattern observed across island replicates in 2010 (Stuart et al. 2014) disappeared. This is explainable at least in part by the fact that we sampled only six islands in 2019, whereas Stuart et al. (2014) sampled 11 islands in 2010. Subsampling all possible combinations of three one-species islands and three two-species islands from data collected in 2010, we found that the effect sizes of the differences in toepad morphology between one- and two-species islands are comparable in 2019 relative to 2010, suggesting low statistical power as an explanation. Nevertheless, the fact that it matters which and how many islands were sampled underscores island-to-island variability in the toepad response to perch height use.

Third, despite a large increase in perch height on the two-species control islands from 2010 to 2019 (Table 2.3), we did not see an increase in toepad size or lamellae number through time on two-species islands relative to one species islands (Tables 2.4 and 2.5). This finding that dynamic and highly consistent behavioral interactions do not lead to equally striking morphological character displacement suggests two possibilities. One, toepad evolution lags behind behavioral change. Though toepad evolution is inferred to be fast in this system (Stuart et al. 2014), perhaps Channel and Yang, for example, only recently experienced an increase in *A. sagrei* density (see discussion below), and *A. carolinensis* are therefore still evolving toward new optima. Two, perhaps the long-standing adaptive assumption of a finely-tuned and selection-driven correlation between perch height and toepad morphology in this system is wrong. Although this correlation holds across *Anolis* species (Glossip and Losos 1997, Macrini et al. 2003), past research on these relationships within species of *Anolis* has been equivocal and remains in need of both conceptual and empirical synthesis (Irschick and Losos 1998,

Irschick and Losos 1999, Sathe and Husak 2015, Kamath and Losos 2017). Specific questions that remain unanswered include: How much of a fitness advantage do *A. carolinensis* gain from having larger toepads or more lamellae, what is the shape of the fitness function, and to what extent does an advantage depend on the frequency and nature of their encounters with each other, with *A. sagrei*, and with other members of their ecological community (*e.g.*, predators)? Answering these questions will assess the utility of character displacement *as a process* in explaining both the rapid morphological evolution and repeated adaptive radiation for which *Anolis* lizards are well-known.

In general, there is growing evidence of fuzzy relationships between behavioral responses and other phenotypic traits that have long been thought of as tightly linked under character displacement. Indeed, Germain et al. (2018) have argued that an approach to character displacement that focuses on specific traits and trait correlations is both limited and biased, and instead suggest focusing on quantifying the competition that is central to character displacement using invasibility experiments. Nevertheless, they acknowledge that such experiments are not always feasible or ethical, particularly for animal taxa. Thus, more nuanced observational research on the day-to-day and generation-to-generation processes of character displacement remains necessary, and we posit that expansive spatiotemporal sampling efforts such as ours represent an important step.

Changing species interactions and habitat use

One avenue for building a nuanced understanding of character displacement in this system is to focus on how interactions between individual *A. carolinensis* and *A. sagrei* change through time. For example, interspecific individual interactions likely become more frequent with increasing population density. Across islands in 2019, *A. carolinensis* perch height was positively related to *Anolis sagrei* density (Figure 2.3; consistent with Prediction 3a). And, we found that, on two-species islands, a greater proportion of individual *A. carolinensis* were located nearby to an *A. sagrei* individual in 2019 compared to 2010 (61% vs. 24%), consistent with an increase in *A. sagrei* density from 2010 to 2019 (though see below for methodological considerations). Thus, we tentatively attribute the continuing upward shift of *A. carolinensis* on two-species control islands to increases in *A. sagrei* density. We speculate that the initial perch height increase in *A. carolinensis* incited by *A. sagrei* arrival is a first step in a series of potential subsequent perch height shifts, which are modulated by changes in *A. sagrei* population density over multiple generations.

Although a correlation between *A. carolinensis* perch height and *A. sagrei* density explains variation in population-level behavior across islands, this correlation alone does not pinpoint a specific

mechanism underlying negative interspecific interactions. Support for our hypothesis that direct, agonistic interactions contribute to shifts in *A. carolinensis* perch height appeared equivocal; in 2019 *A. carolinensis* perched 52cm higher when *A. sagrei* individuals were spotted within a 1m-radius of the focal lizard (consistent with Prediction 3b), but in 2010 the correlation between local *A. sagrei* presence and *A. carolinensis* perch height was negative (in contradiction with Prediction 3b) (Figure 2.4). Although direct interference does occur between these species and appears to be asymmetric in favor of *A. sagrei* (Edwards and Lailvaux 2013, Culbertson and Herrmann 2019), there is also evidence for both resource competition and intraguild predation in this system (Campbell 2000, Gerber and Echternacht 2000). In particular, *A. sagrei* do prey on *A. carolinensis* hatchlings (Campbell 2000), which could select for individuals that either learn to perch higher or that do so instinctively. The relative importance of these interactions in driving habitat shifts and subsequent character displacement warrants continued exploration (Grether et al. 2017, Stuart et al. 2017).

Why did we see evidence for interference competition in 2019 but not 2010 (Figure 2.4)? Several methodological and biological explanations are possible. First, we note that our methods for locating nearby *A. sagrei* upon observing an *A. carolinensis* were implemented far more rigorously in 2019 than in 2010. A more rigorous search for *A. sagrei* upon observing *A. carolinensis* could also partly explain the large increase from 2010 to 2019 in the number of observations of *A. carolinensis* where *A. sagrei* was detected nearby (from 24% to 61%). Our efforts were more focused in 2019 in part because intervening research (Culbertson and Herrmann 2019) suggested that the importance of interference competition in this system has been overlooked. We acknowledge that it is convenient that our more rigorous effort to search for *A. sagrei* coincided with obtaining the results we predicted and that it is possible that our more targeted focus on interference competition unconsciously biased our data collection in 2019. More generally, this reveals a challenge of long-term field research—how can we update and refine our hypotheses to take full advantage of repeated data collection while maintaining methodological consistency and guarding against confirmation bias?

Potential biological explanations also exist for opposite effects of nearby *A. sagrei* presence on individual *A. carolinensis* perch height in 2010 and 2019. These biological explanations illuminate some compelling directions for furthering our understanding of character displacement in this system. First, sex seems to be interacting with local *A. sagrei* presence to predict *A. carolinensis* perch height differences across years. That is, in 2010, nearby *A. sagrei* presence did not influence *A. carolinensis* perch heights but sex did. In 2019, sex had no effect, but nearby *A. sagrei* did. Male and female anoles differ in myriad aspects of their ecology (Lister and Aguayo 1992, Nunez et al. 1997, Butler et al. 2000),

and are likely to interact differently with a congeneric competitor. Dissecting these differences might provide another way to understand the processes underlying non-repeated variation in perch height shifts and morphological character displacement. Second, density-dependent changes in *A. sagrei* behavior (*e.g.*, increased aggression at higher densities) might have altered the nature of interactions between the two congeners, precipitating an emergent shift in how *A. carolinensis* respond to *A. sagrei* (Peiman and Robinson 2010).

2.6 Conclusion

This study was motivated by the observation that *A. sagrei* arrived on South Twin Island after baseline data were collected on resident *A. carolinensis* in 2010. Would character displacement by *A. carolinensis* proceed on this island as it had between 1995 and 2010 on other islands in Mosquito Lagoon (Stuart et al. 2014)? Yes, but with an important qualification. *A. carolinensis* on South Twin now perch higher and have larger toepads, but these changes on South Twin are on par with background changes by *A. carolinensis* between 2010 and 2019 on islands whose *Anolis* community did not change.

Using replicated sampling across both space and time, we were able to move beyond simply asking whether character displacement occurs and could instead dissect the pattern more finely to reveal underlying processes. We see consistent evidence that co-occurring with a congener drives behavioral shifts across multiple spatial, temporal, and organizational scales, but that subsequent morphological shifts were not as consistent as we expected. Our results make it clear that we need to employ complementary approaches incorporating behavioral, ecological, biomechanical, and quantitative genetic data to better understand the processes by which patterns of character displacement arise and are maintained. Investigating density dependence, sex-based ecological differences, and the underlying functional bases of character displacement hold particular promise.

2.7 Acknowledgements

We thank A. Dougherty for field assistance. We thank M. Legare from the Merritt Island National Wildlife Refuge and K. Kneifl from the Canaveral National Seashore for permission to conduct this work. We thank I. Arpayoglou and staff at Florida's Aquatic Preserve Program for logistical support. We thank M. Collyer for statistical help. All live animal work was conducted according to University of Texas IACUC AUP-2018-00287. This work was funded by NSF DEB-1110521 (a doctoral dissertation improvement

grant to Y.S.) and NSF DEB-1456462 (Y.S.). A.K. is funded by the Miller Institute for Basic Research in Science, and K.G. was funded by a Banting Postdoctoral Fellowship (NSERC).

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Chapter 3

The evolution of ‘ecological release’ into the 21st century

This chapter is published and should be cited as follows:

Herrmann, N. C., Stroud, J.T., & Losos, J.B. (2020). The Evolution of ‘Ecological Release’ into the 21st Century. *Trends in Ecology & Evolution*, 36(3), 206-215.

3.1 Summary

Ecological release, originally conceived as niche expansion following a reduction in interspecific competition, may prompt invasion success, morphological evolution, speciation, and other ecological and evolutionary outcomes. However, the concept has not been recently reviewed. Here, we trace the study of ‘ecological release’ from its inception through the present day and find that current definitions are broad and highly varied. Viewing this development as a potential impediment to clear communication and hypothesis testing, we suggest a consensus definition for ecological release: niche expansions and shifts when a constraining interspecific interaction is reduced or removed. In rationalizing this definition, we highlight the various ways ecological release can unfold and address its potential evolutionary consequences.

3.2 A critical examination of ecological release is overdue

Over a half-century ago, Wilson and colleagues coined several terms to describe how **interspecific competition** (see Glossary) can affect species’ ecology and morphology. Initially, “**ecological character displacement**” was introduced to describe the pattern of competition-driven **niche** divergence and associated morphological shifts of species when in **sympatry**, relative to when in **allopatry** [1]. Subsequently, “**ecological release**” and “**character release**” were used to describe a complementary scenario; an expansion in ecological niche and morphological variation when in

allopatry [2,3]. As such, these concepts are closely related, jointly encompassing a suite of population-level ecological and evolutionary responses to changes in the intensity of interspecific competition [3].

In the years since these terms were introduced, ecological character displacement has received major conceptual overviews [4–8], amassed numerous detailed empirical case studies (reviewed in [4,9,10]), and been explicitly incorporated into modern eco-evolutionary frameworks [11,12]. In contrast, ecological release has attracted relatively little attention. Despite claims that it can prompt major ecological and evolutionary phenomena, such as range expansions [13], morphological evolution [14], and speciation [15], we argue that ideas concerning what ecological release represents are in need of critical examination and development.

Glossary

Term	Definition
allopatry	the state of being separated in space in such a way as to prevent organisms from interacting during normal activity
character release	morphological changes associated with ecological release
density compensation	an increase in abundance per unit area in response to the absence of a competitor, such that the increased abundance compensates for the number or biomass of missing competitors
density inflation	an increase in abundance per unit area which, unlike ‘density compensation,’ does not assume a specific underlying mechanism
ecological character displacement	competition-driven niche and morphological divergence among species when in sympatry relative to when in allopatry
ecological opportunity	the availability of ecologically accessible resources that may be evolutionarily exploited
ecological release (original definition)	population-level niche expansion in response to reduced interspecific competition
ecological release (proposed definition)	population-level niche expansions and shifts when a constraining interspecific interaction is reduced or removed

interspecific competition	competition between populations of different species
	competition within a species; correlates positively with population density if
intraspecific competition	resources are limited
niche	the distribution of habitats and resources used by individuals within a population
	an increase in the niche width a population, as measured by an increase in the
niche expansion	variance of habitats or resources used
niche shift	a change in the mean position of a population along a resource axis
	the state of having no spatial separation such that organisms may interact
sympatry	regularly during normal activity

3.3 The historical conception of ecological release: Niche expansion following reduced interspecific competition

The foundational ideas of ecological release stem largely from the biologist David Lack [16–18], who hypothesized that population density and habitat use of island birds were regulated by interspecific competition. The term ‘ecological release’ was formally introduced two decades later by Wilson [2], who in his studies of Melanesian ant communities noted that on islands with lower species richness, species that are forced into marginal, coastal habitats on species-rich islands instead “penetrate the inner forest, mount dense populations there, and fill the available nesting sites.” He attributed this pattern to “the role of interspecific competition” limiting resource use in sympatry.

Wilson’s original description encompasses two population-level responses to reduced interspecific competition: **niche expansion** – an increase in the breadth of habitats or resources used– and **density compensation** – an increase in population density. However, Wilson himself later explicated the relationship between these two responses, treating niche expansion as related to, but distinct from, density compensation [3]. A trend toward marrying “ecological release” with niche expansion and distinguishing it from density compensation took hold in the 1970s [19–21], continued into the 1980s

[22–24], and is supported by more recent empirical and theoretical works (Box 3.1 at the end of the main text).

Though the issue of niche expansion versus density compensation has received explicit attention, there are other, implicit aspects of how ecological release was historically defined and studied that we believe are underappreciated. For example, comparative studies in the 1960s and 70s often tested for ecological release in focal species by measuring whether their population-level variances in habitat use or diet were higher in the absence of competitors [25–29]. Thus, an early defining feature of ecological release was its focus on niche *expansions* as opposed to **niche shifts**. This variance-centric approach has become well-entrenched even though shifts in mean resource are also a common feature of ecological release (described in detail below).

An additional aspect of ecological release often overlooked, perhaps because researchers have long been interested in the evolutionary consequences of ecological release, is that ecological release itself was commonly interpreted as a purely ecological phenomenon; niche expansion following a reduction in interspecific competition need not be the result of evolution [30]. Concurrent with early comparative tests for ecological release, manipulative field experiments in the 1960s and 70s that reduced or removed competitors often demonstrated that the consequent niche expansion can occur within a single generation (reviewed in [31]).

3.4 The evolution of ‘ecological release’: Current conceptions are highly varied

In keeping with the dominant paradigm of ecology at the time [32], ecological release was initially conceived as a response—niche expansion, primarily—to reduced interspecific competition. To determine how researchers have recently defined and contextualized ecological release, we surveyed peer-reviewed publications containing the phrase “ecological release” (105 studies; see Appendix 1) in the period 11/8/18–3/24/20.

We find that recent studies vary substantially in what is accepted as a potential identifier of ecological release. The most frequently mentioned signal was niche expansion (44.8% of studies; Figure 3.1A). However, some studies considered density compensation (22.9%) and morphological change (including both increased variation and mean shifts; 23.8%) as potential evidence for ecological release. Lineage diversification (i.e. speciation), though seldom taken as direct evidence for ecological release, was mentioned in 17.1% of studies. In addition, 28.6% of studies accepted multiple potential identifiers of ecological release (e.g. both niche expansion and morphological change) and 13.3% specified none.

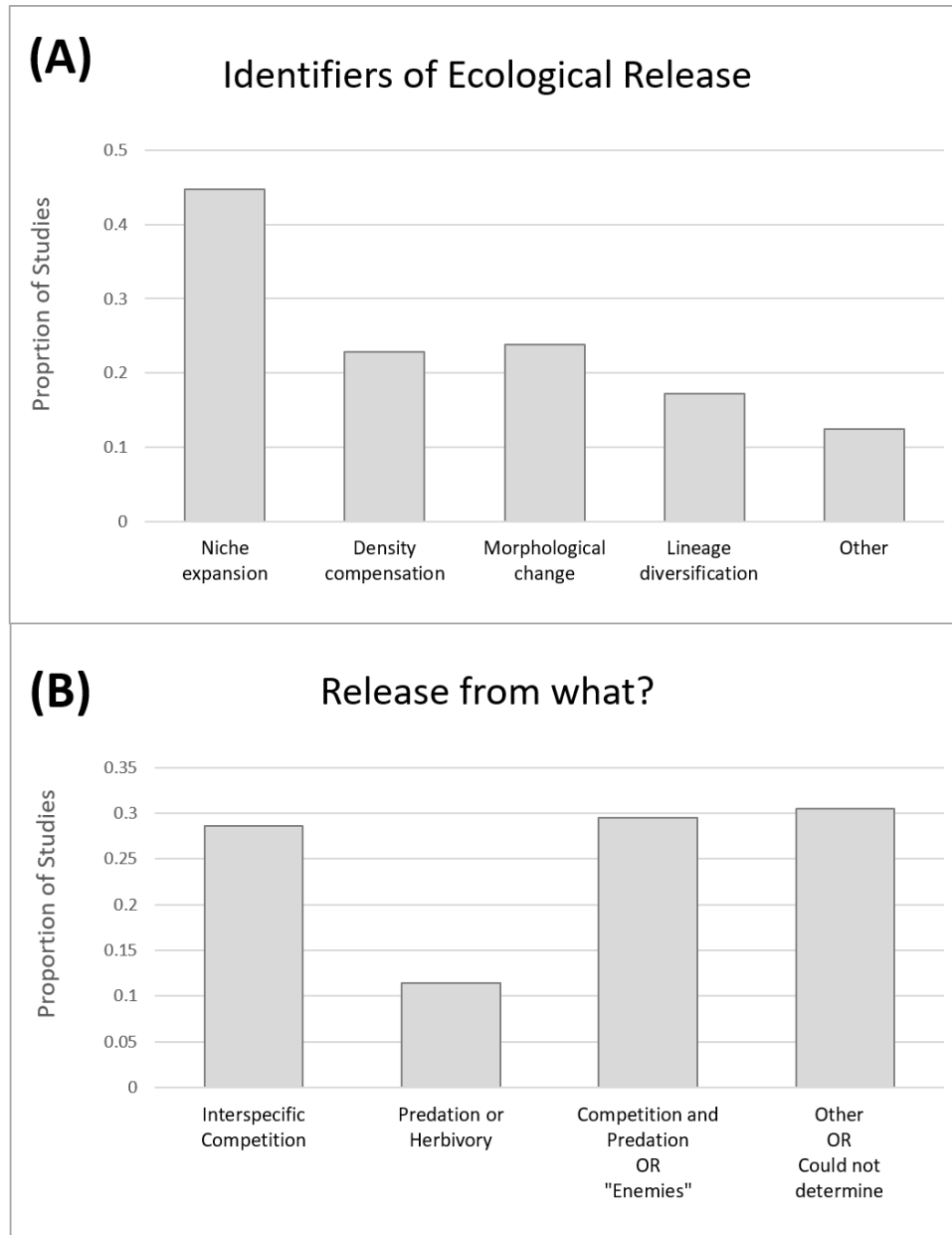


Figure 3.1: According to 105 recent studies, what is ecological release? (A) Studies varied in what they accepted as identifiers that ecological release had occurred, though in corroboration with Wilson’s definition ecological release [2], niche expansion – an increase in resource use breadth - was the most mentioned identifier. Note that the proportions do not add to 100%, as some studies accepted multiple indicators (e.g. both niche expansion and morphological change) while others mentioned no specific indicators of ecological release. See Online Supplementary Material Table S1 for details. **(B)** Studies varied in the mechanisms they identified as underlying ecological release. Most authors implied or stated that ecological release resulted from a relaxation of pressures imposed by antagonists, including competitors, predators, parasites, pathogens, or some combination thereof.

Current definitions of ecological release have also expanded to include multiple underlying mechanisms. Only 28.6% of studies aligned with Wilson [2] in their narrow focus on release from interspecific competition (Figure 3.1B). Other studies tended to focus on release from predation or herbivory (11.4%) or from interspecific antagonists in general, including competitors but also predators, parasites, and pathogens (29.5%; Figure 3.1B). This broadened definition was common among the substantial portion of studies that described ecological release in the context of anthropogenic environmental change (36.2%; Appendix 1). For example, several studies explored whether ecological release explained invasion success of some non-native species (i.e. the ‘enemy release hypothesis’; [33]). Additionally, multiple studies either acknowledged or directly investigated ways in which other anthropogenic changes, including habitat modification, climate change, and overhunting or overfishing, might alter community composition and lead to ecological release (Appendix 1). One study [34] associated ecological release with positive interspecific interactions, such as facilitation and mutualisms, which can drive niche expansion via amelioration of environmental stressors [35,36]. In its broadest conception, ecological release was described as a relaxation of “constraining selective pressures” [37].

3.5 Defining ecological release in the 21st century

That the definition of ecological release varies widely depending on whom you ask is problematic. To facilitate communication and effective hypothesis testing, we propose the following definition for **ecological release**: niche expansions and shifts when a constraining interspecific interaction is reduced or removed.

Moving beyond interspecific competition

In the days of Lack and Wilson, interspecific competition was seen as the primary force structuring ecological communities, and thus it makes sense that the idea of ecological release was presented in that context. Researchers now widely accept that other biotic factors can constrain a

population's resource use, resulting in acknowledgement that niche expansion may occur during "ecological release from predation" or "ecological release from parasitism."

One could expand the idea even further, as there are many additional ecological mechanisms that can promote niche changes. These include positive interspecific interactions such as facilitation and mutualisms [34–36], an increase in the local supply of resources [38,39], and changes in abiotic (e.g. climatic) conditions that provide access to previously inaccessible resources [40]. We suggest that, rather than broaden the possible mechanisms underlying ecological release so much that its original meaning becomes unrecognizable, we use the term only to describe the direct release from constraining, negative interspecific interactions (i.e., competition, predation, parasitism, pathogenicity). We acknowledge that this release itself can have different proximal causes, including but not limited to establishment in a new geographic area, extinction of an antagonist, or a surge in local resource availability.

What should count as potential evidence that ecological release has occurred?

The term 'density compensation' reflects its traditional association with interspecific competition (the increased density *compensates* for the number or biomass of reduced competitors; [20]). As we propose extending the definition of ecological release to include additional negative interspecific interactions, the term '**density inflation**,' which describes an increase in density without assuming a specific mechanism, is an appropriate substitute for 'density compensation' [23]. However, we have already discussed the historical precedent for and rationale behind distinguishing niche expansion (and 'ecological release') from density responses. Thus, there are two outstanding issues which we explore below: 1) Why we break from tradition in accepting both population-level niche expansions (increases in resource use variance) *and* niche shifts (changes in mean resource use) as potential evidence for ecological release; 2) Why many authors have subsumed distinct evolutionary

phenomena (namely, morphological evolution and diversification) into ‘ecological release,’ and why we choose not to.

3.6 Niche dynamics of ecological release: Population- and individual-level responses

We favor a framework for describing niche changes during ecological release which evaluates means and variances, jointly, at the levels of both populations and individuals (Figure 3.2). Using this framework, we can generate specific predictions about how ecological release might affect the evolution of traits other than the niche itself (see next section).

First, we suggest that during ecological release, a population may undergo a niche expansion, niche shift, or both. For example, if a species of consumer were introduced to a new community with similar prey resources but fewer competitors, the population may expand resource use to consume both larger and smaller prey without changing its mean niche position. However, if new resource availability is asymmetrically distributed, then a shift in population mean niche position may occur as resource use broadens. Several of the ecological release patterns described in the 1960’s and 70’s, including Wilson’s original description of niche expansion in Melanesian ants [2], were also accompanied by such directional niche shifts [25,27,29], though this did not prevent the term ‘ecological release’ from becoming almost exclusively associated with variances. That niche shifts without expansion (e.g. [41,42]; Figure 3.2A) have not historically qualified as ecological release may reflect semantic tradition more than biological reality (Box 3.2 at the end of the main text). Alternatively, niche shifts without expansion may be rare and ephemeral; even if many individuals switch to preferred, newly available resources, some individuals will still benefit from using old resources, especially if the preferred resources become depleted [43].

Second, we acknowledge that population-level niche expansion during ecological release can be the result of several different patterns at the individual level. One possibility is that population-level

niche expansion proceeds via a widening of individual-level niches to include newly available resources ('parallel release'; [44]). Another possibility is that population-level niche expansion proceeds via individuals diverging in their mean niche position while maintaining relatively narrow individual niche widths, resulting in a population of individuals specializing on different parts of the resource spectrum (the 'niche variation hypothesis'; [45]). These possibilities, which can manifest from behavioral plasticity in a single generation or individual-level niche evolution over multiple generations [44,46], represent opposite extremes but are not mutually exclusive. Furthermore, either can lead to population-level expansion around a stable mean (Figure 3.2B and C) or accompanied by a niche shift ([47]; Figure 3.2D and E).

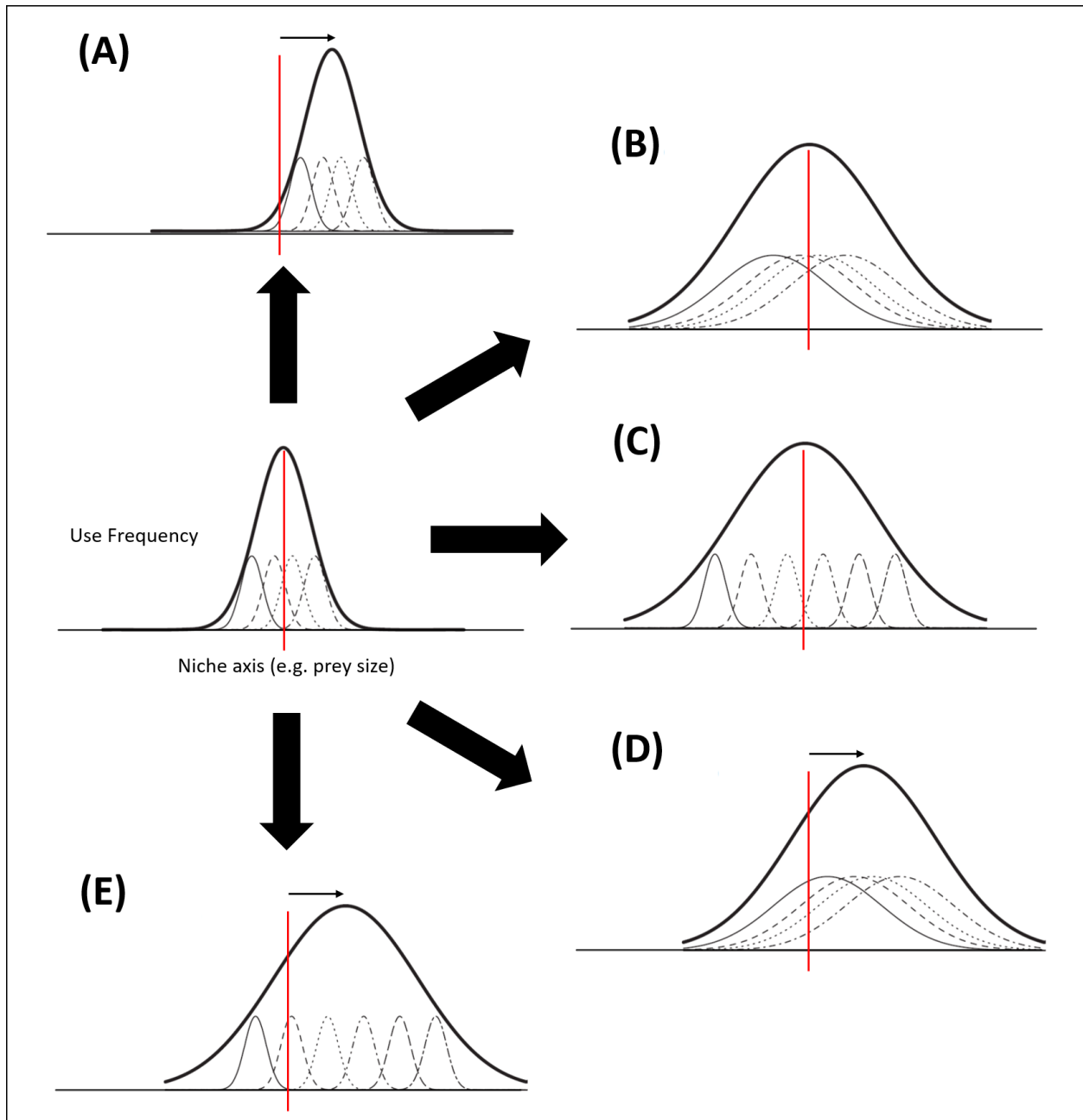


Figure 3.2: Five scenarios illustrating niche responses during ecological release from the same hypothetical initial state. Dashed black lines are the niches of individuals within the population (solid black line). The vertical red line represents the mean niche position in the initial state. **(A)** Although population-level niche shifts without expansion did not historically qualify as ecological release, we recognize this scenario as a potential response to a reduction in biotic constraints. A population may also experience ecological release via **(B)** within individual niche expansion and with no population-level niche shift **(C)** between individual niche expansion and with no population-level niche shift **(D)** within individual niche expansion along with a population-level niche shift **(E)** between individual niche expansion along with a population-level niche shift.

3.7 The evolutionary consequences of ecological release

Morphological evolution (formerly known 'character release')

Ecological release has long been hypothesized to have multiple potential evolutionary consequences. For example, MacArthur and Wilson [3] introduced the term 'character release' to describe morphological evolution exhibited by populations assumed to have undergone ecological release. As originally envisioned, character release can manifest in two ways; (i) an increase in morphological variation, for example if a bird population experiencing ecological release has a broader diet and also exhibits increased bill size variation [45], or (ii) a morphological mean shift, for example if a bird population experiencing ecological release with a directional bias toward consuming larger prey items also exhibits an increase in average bill size [30,48].

With the potential for ecological release to take many forms (Figure 3.2), it is unsurprising that associated morphological changes can also vary. For example, we might expect shifts in morphological means only when ecological release is accompanied by a niche shift (Figure 3.2A, D, and E). Additionally, increases in morphological variation may be more common when niche expansion proceeds via individuals diverging in their mean niche position, as the population will ultimately comprise individuals that specialize on different and relatively narrow segments of the resource spectrum (Figure 3.2C and E). If instead, individuals simultaneously broaden their resource use such that their individual niches overlap substantially (Figure 3.2B and D), selection may not favor increased morphological variation.

Yet these scenarios are hypotheses to be tested. Morphological evolution, even that which is consistent with patterns originally described by MacArthur and Wilson [3], should not be accepted as *prima facie* evidence that ecological release has occurred because other processes may cause the same evolutionary outcome. As use of the term 'character release' has mostly stopped (Appendix 1), we ask that the field take care to distinguish morphological evolution from 'ecological release,' which should be reserved for describing niche changes.

Adaptive Speciation

In recent years ecological release has become an essential component of conceptual models that posit how **ecological opportunity**—loosely defined as the availability of ecological resources that can be evolutionarily exploited—can ultimately promote adaptive diversification [4,49–51]. By and large, these models posit that if ecological release leads to increased and heritable trait variation on which selection can subsequently act, a species may be primed to diverge into distinct forms that later become reproductively isolated. If this process occurs repeatedly within a lineage across time or space, it manifests as adaptive radiation.

Conceptual and theoretical models may propose links between ecological release and adaptive speciation, but they do not equate them—the former can occur without the latter. Indeed, there may be conditions under which ecological release precludes rather than prompts speciation, such as when it promotes gene flow between populations that might otherwise remain distinct [52]. Ecological release is one of many potential primers of diversification but remains a hypothesis to be evaluated against other contenders.

Experimental microbial systems are perhaps the most amenable to direct tests of the proposed mechanistic links between ecological release and adaptive diversification [53], as empirical studies in nature must often infer whether ecological release in the past is responsible for present diversity. However, it may be possible to bridge this process-pattern divide by exploring whether ecological release in extant clades is more likely to occur along some niche axes (e.g. microhabitat, macrohabitat, diet) than along others, and whether these are the same axes that tend to define patterns of adaptive diversification [54]. Theoretical studies that explicitly investigate the relationship between niche width evolution and diversification (e.g. [55]) should inform the design and interpretation of empirical work. Additionally, more studies of all types should simultaneously consider the effects of ecological release along multiple niche axes, as expansion along one axis may alter evolution along another [56,57].

3.8 Concluding remarks

There is a rich collection of outstanding conceptual questions, spanning topics in ecology and evolution, related to how populations respond to a reduction in biotic constraints (see Outstanding Questions below). Tackling them will require collaboration and clear communication.

By investigating ecological release with a critical lens, we discovered a lack of consensus around exactly what it represents. We hope that our proposed definition for ecological release – niche expansions and shifts when a constraining interspecific interaction is reduced or removed – along with the discussion we have provided, will ultimately lead us to a sharper understanding of what ecological release is and, by extension, how it might be studied.

Box 3.1: Density compensation may cause niche expansion, but it does not have to

Density compensation can be the proximate cause of niche expansion during ecological release. If **intraspecific competition** increases with population density, then population-level niche expansion may occur as preferred resources become limited, favoring individuals using habitats and resources that were previously sub-optimal [44,58,59]. However, it is also possible for increasing intraspecific resource competition to initially reduce, rather than expand, the range of resources used by a population [60]. Empirical and theoretical evidence suggest that the outcome depends on both resource availability and consumption rates; when favored resources are depleted quickly and sub-optimal resources are either inaccessible or extremely inefficient to consume, a population may exhaust subsets of its original niche without incorporating new types of resources [55,61,62]. Under these conditions, density compensation leads to narrowing of the niche, at least temporarily. For example, alewife (*Alosa pseudoharengus*), which are efficient consumers in eastern North American lakes, exhibit a negative relationship between population density and diet variation in both natural and experimental settings [63].

Alternatively, niche expansion during ecological release can also occur without density compensation; prior to any density response, extant individuals may choose to use resources from which they were previously excluded, either because these resources are inherently more valuable than previously used resources or because they have become relatively more valuable in the absence of costs no longer imposed by the presence of antagonists [44].

It is possible, therefore, for density compensation to either promote niche expansion or niche contraction, and for niche expansion to occur in the absence of density compensation. For this reason, we consider density compensation to not be part of the definition of ecological release; rather, the nuances of how density compensation is related to ecological release warrant continued study. Specifically, identifying the conditions under which niche expansion and density compensation fuel each other via positive feedback loops may be a key to determining whether the consequences of ecological release are transient or long-lasting.

Box 3.2: The mean-variance distinction between ecological character displacement and ecological release

Ecological character displacement and ecological release each represent responses to changes in the intensity of interspecific competition. Given their historical ties (having both been formally introduced by Wilson) as well as their conceptual overlap, it may be tempting to assume that the two phenomena are, in a way, opposite. However, we argue that this is not strictly true.

Ecological character displacement refers to niche divergence resulting from interspecific competition that leads to evolutionary shifts in other (mostly morphological) traits (reviewed most recently in [10]; the role of plasticity in these shifts has also been recently discussed [64]). Studies of character displacement focus mostly on means, explicitly predicting that trait shifts represent an evolutionary response to interspecific competition. A classic example is mean beak size divergence

between the large ground finch (*Geospiza magnirostris*) and medium ground finch (*G. fortis*) on Daphne Major driven by competition for limited seeds [65].

Historically, ecological release referred to increases in niche breadth, rather than shifts in mean niche position, and focused primarily on resource use. For example, the Cocos finch (*Pinaroloxias inornata*), isolated from confamilial competitors on its own remote island, exhibits multiple foraging behaviors across a wide range of microhabitats [66]. In contrast to ecological character displacement, the evolutionary consequences of ecological release were not inherent to the term. Therefore, classic conceptions of ecological character displacement and ecological release were distinct in at least two ways: the former focused on mean niche position and encompassed explicit evolutionary predictions, whereas the latter focused on resource-use variances and represented a purely ecological phenomenon.

The mean-variance distinction between ecological character displacement and ecological release is at least partly historical artifact; it was implicit in the concepts as they were originally described [1,2], and early empirical studies mostly followed suit by focusing on either means (ecological character displacement) or variances (ecological release), but not both. Yet as we demonstrate, shifts in mean niche position sometimes occur during ecological release (see main text). More generally, the mean and variance of a trait can jointly determine how the trait distribution changes in response to selection [67,68]. In this way, the mean-variance distinction between ecological character displacement and ecological release may ultimately obscure our understanding of how populations respond to changes in biotic pressure. Thus, we embrace the possibilities that ecological release may drive niche shifts as well as niche expansions and that either may accompany or lead to evolutionary change.

3.9 Outstanding Questions

- Multiple biotic interactions during ecological release

- How do changes in interspecific competition and intraspecific competition interact to drive niche changes during ecological release?
- What are the relative effects of decreased interspecific competition versus predation on the magnitude of ecological release?
- Exploring the niche dynamics of ecological release
 - How frequently and under what conditions is ecological release accompanied by a niche shift?
 - How frequently and under what conditions does ecological release occur within versus between individuals within a population?
- Understanding the eco-evolutionary dynamics of ecological release
 - What is the role of plasticity in ecological release?
 - How does natural selection operate during ecological release?
 - Is evolutionary change more likely to accompany ecological release along certain niche axes (e.g. macrohabitat, microhabitat, diet)?
 - Under what conditions does ecological release lead to speciation?
- Ecological release and a multi-dimensional niche
 - Does ecological release along one niche axis tend to promote or inhibit ecological release along others?
 - How do the common niche axes along which ecological release occurs differ across taxa, and do these axes of release correlate with the niche axes along which taxa tend to diversify?
- Ecological release in the Anthropocene
 - Is ecological release more common in human-altered environments?
 - To what extent is ecological release responsible for the success of invasive species?

3.10 Acknowledgements

We thank David Haig, Ambika Kamath, Yoel Stuart, and four anonymous reviewers for providing helpful feedback on the manuscript.

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Chapter 4

Ecological release analyzed among individuals, across two generations, and along multiple niche axes in *Anolis carolinensis*

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Associated data and R script are available from GitHub

(<https://github.com/NCHerrmann/EcologicalRelease/>)

4.1 Summary

A population freed from a constraining interspecific interaction (e.g. competition or predation) may experience niche shifts and expansions. This phenomenon, termed ecological release, is an evolutionary process driven by individual behaviors and inter-individual interactions. However, empirical studies of these interactions seldom observe them directly, instead inferring process from pattern. Here, we set up experimental conditions for ecological release of the lizard *Anolis carolinensis* from constraining interactions with its congener, *A. sagrei*, by constituting populations of lizards on small islands. We monitored individual and population habitat use along three niche axes (perch height, perch diameter, and lateral movement between perches) on one experimental (one-species) and one control (two-species) island, for three time periods: 1) Pre-removal, when both islands had both species; 2) Post-removal, shortly after *A. sagrei* were cleared from the experimental island; 3) Delayed post-removal, seven months later, when long-lived lizards were joined by a second generation, born in the intervening months. We found that ecological release led to a decrease in green anole perch height. This shift did not occur during Post-removal but was evident by Delayed post-removal, when both generations on the one-species island were perching nearly 130cm lower than their counterparts on the two-species island. We also documented correlated increases in perch diameter at both the individual

and population level but no changes in the extent of individuals' lateral movement. Lastly, changes in population-level niche width (i.e. perch height and diameter variances) occurred without detectable changes in niche overlap among individuals. Our results demonstrate that the dynamics of ecological release in nature need not be inferred, because experiments can observe them directly at level of individuals, across generations, and along multiple niche axes.

4.2 Introduction

A central challenge of eco-evolutionary dynamics is understanding how patterns of trait variation and species diversity emerge from processes that involve individual behaviors and inter-individual interactions (Pelletier et al., 2009; Hendry, 2017; Romero-Mujalli et al., 2019). Indeed, a suite of phenomena that link patterns and processes across levels of biological organization—including character displacement, reinforcement, and other mechanisms of diversification—have made up the core of evolutionary ecology for decades (reviewed in Schluter, 2000; Pfennig and Pfennig, 2012). Ecological release, defined as niche expansions and shifts when a constraining interspecific interaction (i.e. competition, predation, parasitism, pathogenicity) is reduced or removed, is one such phenomenon (Herrmann et al., 2021).

The process of ecological release and the patterns it is thought to generate have been studied empirically at the population level for over half a century (Connell, 1961; Wilson, 1961; Crowell, 1962; Paine, 1966). More recently, how changes in individual behavior drive ecological release has been inferred by observational studies comparing individual-level niche variation across populations that differ in, for example, number of purported competitors (Costa et al., 2008; Cloyd and Eason, 2016; Costa-Pereira et al., 2019; Rainville et al., 2021). However, we have almost no direct field observations of individual responses during the initial stages of ecological release. Partly, the challenge is due to the

difficulty of observing the process in action—in natural populations, by the time one notices evidence of ecological release, it is either well underway or thought to have occurred in the distant past.

Experimentally generating the conditions that cause ecological release in natural settings can address this challenge. For example, Bolnick et al. (2010) experimentally induced ecological release in stickleback, deployed for 15 days in mesh enclosures in natural lakes, by comparing control populations in the presence of two interspecific competitors to experimental populations where one or both competing species were removed. Crucially, such a set up allowed the authors to demonstrate that ecological release alters stickleback diets on behavioral timescales (within the lifetimes of individual fish), that individuals can change their diets in response to competitor removal even while the population-level niche remains stable, and that release from different competing species can have different effects. Still, numerous questions about the eco-evolutionary dynamics of ecological release remain largely untested by field experiments. For example, how does ecological release affect individuals across multiple niche axes instead of a single axis (MacArthur and Wilson, 1967)? Also, how do niche changes during ecological release compare across subsequent generations, and what does this suggest about the roles of plasticity versus evolution during the initial stages of ecological release?

Lizards in the genus *Anolis* (anoles) are a compelling system for studying the process of ecological release. Individuals within a population have been shown to differ along three niche axes that define their largely arboreal habitat use: perch height, perch diameter, and the lateral extent of their movement among perches (Kamath and Losos, 2017a; 2018). Furthermore, interspecific competition appears to drive habitat partitioning among co-occurring species (reviewed in Losos, 2009), and field experiments that manipulate competitor presence or density consistently demonstrate population-level niche changes (Pacala and Roughgarden, 1985; Rummel and Roughgarden, 1985; Leal et al., 1998). However, such experimentally induced niche changes are yet to be dissected at the level of individuals, across generations, or along more than two niche axes.

Here, we describe a field-based, experimental test for ecological release in *Anolis carolinensis* (green anole). In southern Florida, green anoles perch higher where they overlap with introduced *Anolis sagrei* (brown anole; Stuart et al., 2014). This constraining interspecific interaction appears to have several underlying mechanisms, including resource competition for arthropod prey (Campbell, 2000), direct aggression (Culbertson and Herrmann, 2019), and intraguild predation (Gerber and Echternacht, 2000). We hypothesized that the experimental removal of brown anoles would lead to a decrease in green anole mean perch height (niche shift), an increase in perch height variance (niche expansion), or both. We tested for these changes across two generations and compared them to those experienced by green anoles in continued sympatry with brown anoles. To capture the potential multi-dimensionality of niche changes, we also tracked individuals along two other axes that describe habitat use in anoles: perch diameter, which often distinguishes species that occupy distinct microhabitats, but is relatively understudied at level of individuals within populations (Losos, 2009; Kamath and Losos, 2017a), and the lateral extent of individuals' movements among perches, which can affect access to food and potential mates and may be modulated by the avoidance of interspecific interactions. Finally, we explored each niche axis at both the individual and population levels, with the goal of understanding the individual behavioral processes that underlie population patterns of ecological release.

4.3 Methods

Study sites and populations

The experiment was conducted on two islands – SL1B (0.04 ha; 27°29'36.5"N, 80°19'42.0" W) and SL13C (0.03 ha; 27°32'45.5"N, 80°20'34.0" W; Figure 1) – which belong to a chain of low-lying islands in Florida's Indian River Lagoon. The islands were created about 60 years ago from dredge spoil, a byproduct of the US Army Corps of Engineers deepening the channel that runs through the lagoon (Campbell, 2000). Despite their small size, both study islands have vegetation similar to that of larger

islands nearby; they contain a mix of open areas and closed-canopy stands with several trees exceeding four meters in height, most commonly red mangroves (*Rhizophora mangle*), black mangroves (*Avicennia germinans*), and Brazilian pepper (*Schinus terebinthifolia*).



Figure 4.1 The two islands used for this experiment, SL1B (left) and SL13C (right)

Green and brown anoles have established themselves on most dredge spoil islands in the lagoon, including several islands smaller than 0.05 ha. However, neither were initially present on our study islands, so we transplanted lizards of both species to establish sympatric populations. These lizards came from larger, nearby islands where both species were relatively abundant (SL12: 27°29'55"N, 80°19'46" W; SL3: 27°32'7"N, 80°20'20" W; IR11: 27°48'1"N, 80°27'12" W), with each experimental island receiving a mix of individuals from each source island. Green anoles from our source populations have lived in sympatry with brown anoles for at least 25 generations (Campbell, 2000).

Experiment establishment and timeline

We established study populations on SL1B and SL13C in May 2018. Individuals were captured from source islands by lasso or by hand, transported to field housing for processing, and released at a randomly selected location on either SL1B or SL13C within 48 hours. Green anoles received a unique bead tag sewn into the tail (Fisher and Muth, 1989). To help identify individuals that lost their bead tag,

we also inserted a UV-fluorescent alphanumeric tag (Northwest Marine Technology, Inc.) subcutaneously in each hindlimb. Because bead tags may increase the visibility of a lizard to potential predators, brown anoles also received bead tags even though they were not the focus of this study. Transplanted populations of both species were established with a 1:1 sex ratio and at naturally occurring densities (~500 individuals/ha for green anoles and ~1000 individuals/ha for brown anoles; Campbell, 2000). Once target densities were reached, the populations were given four weeks to acclimate to the experimental islands prior to field observations.

Subsequent observations of green anole habitat use occurred in three stages, each of which lasted approximately three weeks: Pre-removal, when both islands had both species (July 2018); Post-removal, shortly after *A. sagrei* were cleared from one island (August 2018); and Delayed post-removal, seven months later (March 2019). During the Pre-removal stage (July 2018), both islands contained both species. Then, we flipped a coin to determine which island would have its brown anoles removed. It took two days to remove the brown anoles from SL13C (hereafter, “one-species island”), which were caught by lasso or by hand. We spent an equal number of hours those days walking around SL1B (hereafter, “two-species island”), but did not remove any brown anoles. The Post-removal observation stage (August 2018) began two days later.

Study populations were observed again during the Delayed post-removal stage (March 2019). At this time, the one-species island still had only green anoles and the two-species island still had both species. However, populations on both islands were a mix of old individuals, measured and tagged in 2018, and a generation of new, yet untagged individuals born on the study islands (young of the year). We captured new green anoles on both islands and processed them identically to individuals from the previous year.

Measuring the niche

We used the same protocol to quantify green anole habitat use on both islands during the Pre-removal, Post-removal, and Delayed post-removal stages. Upon arriving at an island, a team of two or three people would scan the site for green anoles using binoculars, first by wading in the shallow water surrounding the island and then by traversing the interior. When a green anole was spotted and undisturbed by our presence, we recorded the individual's unique bead tag ID and its habitat use along three axes – perch height, perch diameter, and lateral location – in a manner described below. Only the first observation of each individual was recorded during a visit.

Visits occurred during daylight hours when lizards were active (7:30-18:00). Total time per visit varied based on the number of observations and was seldom longer than an hour. Visits usually occurred in pairs between islands (one-species island followed by two-species island or vice versa), and all same-day visits to a site were separated by at least one hour. We typically alternated which island we visited first to ensure that the sites received similar representation across times of day. We also approximately equalized the total number of person-hours per island (search time x number of people) during each stage (Pre-removal: ~68 person-hours per island, Post-removal: ~68 person-hours, Delayed post-removal: ~49 person-hours).

Green anole perch height and perch diameter were recorded to the nearest cm. Perch heights above 150cm were measured with digital measuring pole (Sokkia, Inc.) that can extend up to eight meters. Lizards observed on the ground were noted as such and were not assigned a perch diameter at the time.

To track the extent of individuals' lateral movement, we laid out a grid of 2x2m squares on each island using small flags (one-species island: 78 squares, two-species island: 62 squares) and recorded the grid location of each green anole observation. Outer grid squares extended at least to the water's edge. In areas where tree limbs protruded over the water, we marked grid vertices by tying small pieces of flagging tape to branches.

Statistical analyses

Perch height

To compare population perch height means across islands and experimental stages, we ran a linear mixed effects model (using the *lme* function in the R package *nlme*) with perch height as the response variable, island-stage combination (e.g. two-species-island during Pre-removal, one-species island during Delayed post-removal) as a fixed effect with six levels, and individual lizard ID as a random effect. To visualize how individuals contributed to population-level perch height means, we calculated the mean perch height for each individual in each session and generated two plots: 1) means for all individuals across all stages, 2) individual mean shifts from Pre-removal to Post-removal. We also conducted three Wilcoxon rank-sum tests on individual perch height means, one for each stage, to test for rank order differences between the two islands.

To compare population perch height variances across islands and experimental stages, we first calculated perch height residuals (deviations) from the mean, separately for each island-stage combination, by subtracting the population's perch height mean from each observed value. We then ran an ANOVA comparing the absolute value of these residuals. This is functionally equivalent to a Levene's test for the homogeneity of group variances, but it allows for post-hoc pairwise comparisons between groups (which a standard Levene's test does not). We used a Tukey's honest significance test to make post-hoc comparisons between island-stage combinations, with p-values adjusted for multiple comparisons using a family-wise error rate.

To compare the degree to which the distribution of individual perch height use differed from the population distribution (i.e. individual niche specialization) across islands and experimental stages, we used the *WTcMC* function in the R package *RInSp* (Zaccarelli et al., 2013) to calculate the total niche width (TNW), the within-individual component of perch height variation (WIC), and the proportion of

total variation nested within individuals (WIC/TNW), separately for each island-stage combination. High WIC/TNW suggests that individual niche widths are similar to population-level niche widths, whereas low WIC/TNW suggests niche differentiation among individual habitat use specialists. The package *RInSp* interprets zeros as missing values, so we added one to all recorded perch heights prior to this analysis. To help interpret differences in WIC/TNW across islands and stages, we ran simulations to determine whether these differences could be explained by sampling error (see Appendix 2 for details).

Perch diameter

We conducted analyses of population- and individual-level changes in perch diameter identical to those described above for perch height. Of 829 total observations, 24 green anoles were perched on the ground. To a small lizard, this flat surface is functionally very similar to the widest perches it may use above the ground, such as a broad tree trunk. Therefore, we assigned all ground observations a perch diameter equal to the largest perch diameter in the data set (24 cm).

Lateral movement

We manually assigned each individual a measure of lateral movement for each session by counting the minimum number of grid squares it must have occupied at some point during that session, based on all of the locations where it was observed. We conducted three Wilcoxon rank-sum tests, one for each stage, to compare the extent of individuals' lateral movement across islands. Unlike individual mean perch height or perch diameter, this metric scales positively with number of observations per individual (see Appendix 2), a confounding factor that we account for in our interpretation of the results.

All analyses were conducted in R version 4.0.2. Data and an annotated R script are available on GitHub (<https://github.com/NCHerrmann/EcologicalRelease/>).

4.4 Results

Sampling summary

In total, we made 356 observations of 24 unique green anoles on the two-species island, and 473 observations of 40 unique green anoles on the one-species island. Table 4.1 breaks down this sampling effort by sex and experimental stage.

Table 4.1 Summary of populations and sampling effort on experimental islands.

	Two-species Island (SL1B)							One-species Island (SL13C)						
	Greens					Browns		Greens					Browns	
	Males Ind.	Females Obs.	Ind.	Obs.	Ind. /ha	Ind.	Ind./ ha	Males Ind.	Females Obs.	Ind.	Obs.	Ind. /ha	Ind.	Ind./ ha
Pre-removal (July 2018)	9	93	7	29	533	30	1000	10	83	11	37	525	40	1000
Post-removal (August 2018)	8	125	6	37	467	27	900	8	107	11	59	475	0	0
Delayed post-removal (March 2019)	5	37	7	35	400	40	1333	14	108	15	79	725	0	0

Perch height

Population mean perch height was statistically indistinguishable across islands during the Pre- and Post-removal stages (Figure 4.2A, Table 4.2). However, in the Delayed post-removal stage, perch height decreased on the one-species island and increased substantially on the two-species island. During this stage, one-species island green anoles were perching nearly 130cm lower than two-species island green anoles on average.

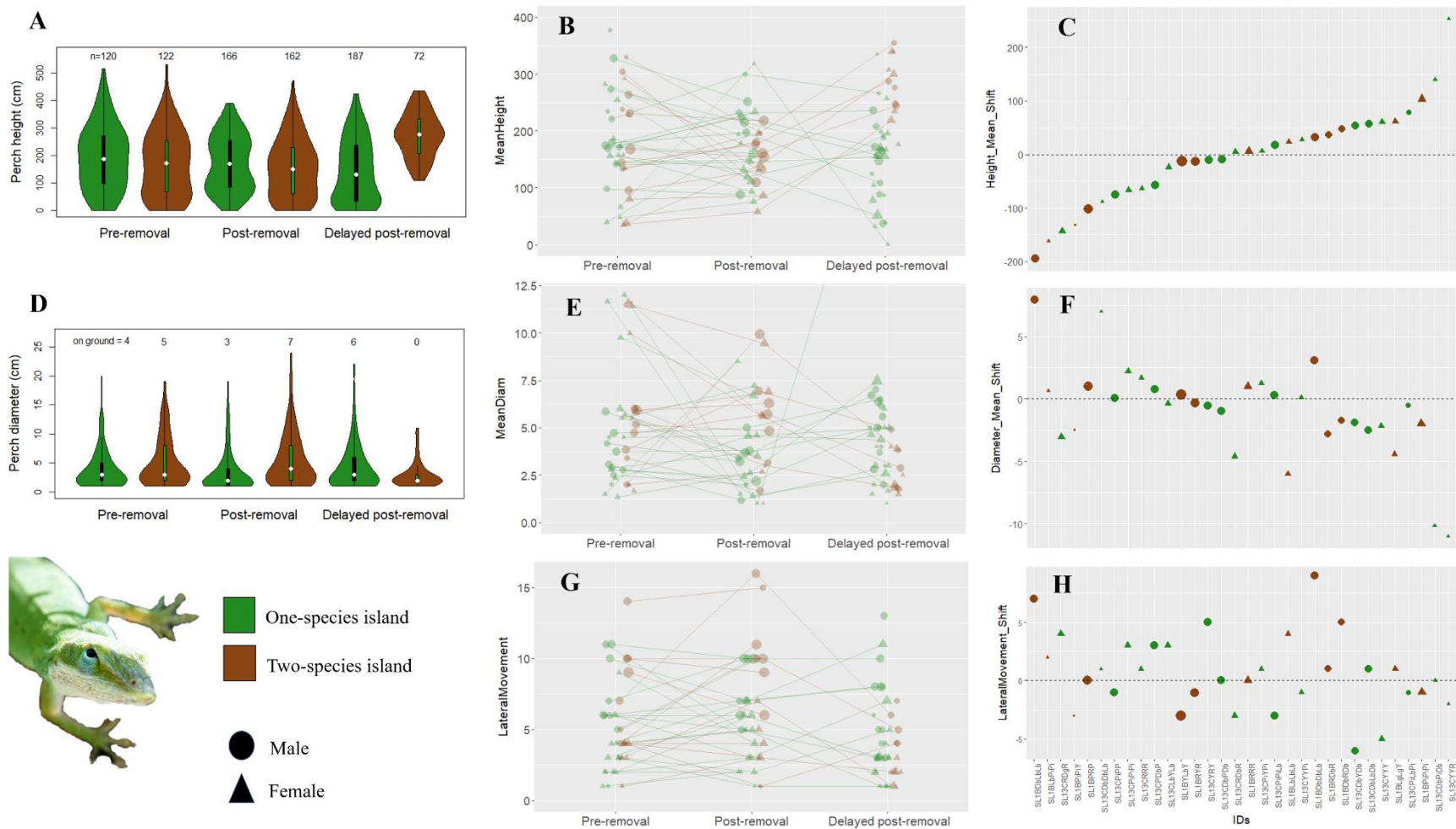


Figure 4.2 Green anole population and individual level niche changes along three axes: perch height (top row), perch diameter (middle row), and the extent of lateral movement (bottom row). **A)** Violin plot depicting all perch heights measured during the experiment, broken down by island and experimental stage. The width corresponds to the density of observations at a given height. The box and whisker plot nested within each

violin depicts the median (hollow circle) and interquartile range (vertical rectangle). **B)** Individual mean perch height for all green anoles across all stages. Each point within a stage represents a unique individual and carries information about the individual's island (color), sex (shape), and number of observations (size). Horizontal lines connect the same individual observed across stages. **C)** Individual mean perch height shifts from Pre-removal to Post-removal for green anoles observed at least once in each stage. These mean shifts are estimates which increase in reliability as observation number increases. However, no error bars are pictured as each point represents the difference of two means, one calculated from Pre-removal observations and the other from Post-removal observations. Individuals are ordered from largest perch height decrease to largest perch height increase. **D)** Same as A, but for perch diameter. Sample sizes are equivalent to those depicted in A. Here, the number above each violin represents the number of ground observations in each group, which are not incorporated into the violin distributions. **E)** Same as B, but for individual mean perch diameter. The line that continues above the field of view connects to a point at 24cm. This female from the one-species island was observed once, on the ground (and was therefore assigned a perch diameter of 24cm), during Delayed post-removal. **F)** Same as C, but for individual mean perch diameter. Individuals on the x-axis are in the same order as C – from largest perch height decrease to largest perch height increase – to visualize the relationship between perch height shifts and perch diameter shifts. **G)** Same as B and E, but for the extent of individuals' lateral movement, measured as the minimum number of unique grid squares a lizard must have traversed based on all the locations it was observed during a particular stage. **H)** Same as C and F, but for the extent of individuals' lateral movement.

Table 4.3 Mixed effects model testing for population-level perch height shifts. Pre-removal stage lizards on the one-species island are the baseline (intercept) of this model. 'Estimated within-island change from previous stage' and 'Estimated difference between islands' are calculated by comparing the relevant coefficients estimated by the model.

		Value	Std. Err.	t-value	p-value	Estimated within-island change from previous stage	Estimated difference between islands (one-species minus two-species)
Pre-removal	(Intercept) One-species island	180	12.9	13.9	< 0.001	NA	11.4
	Two-species island	-11.4	19.5	-0.6	0.56	NA	
Post-removal	One-species island	-10.3	12.3	-0.8	0.4	-10.3	18.9
	Two-species island	-29.2	19.2	-1.5	0.13	-17.8	
Delayed post-removal	One-species island	-31.2	13.4	-2.3	0.02	-20.9	-129.9
	Two-species island	98.7	20.9	4.7	< 0.001	127.9	
Individual ID (Random effect) Standard Deviation: Intercept = 45.5, Residual = 99.5							

Individual lizards varied in the extent to which they changed their perch height across experimental stages (Figure 4.2B). Some individuals underwent large perch height shifts from Pre-removal to Post-removal (Figure 4.2C), though because these extreme individual shifts occurred on both islands and in both directions, population-level distributions remained relatively stable. In contrast, the Delayed post-removal divergence in population-level perch height was driven by consistent, directional shifts at the individual level. During this final stage, mean perch heights for old (long-lived) individuals mostly decreased on the one-species island and ubiquitously increased on the two-species island (compare the slopes of lines connecting individuals observed across stages in Figure 4.2B). Perch height means for new (young of the year) individuals were similarly distinct between islands. Wilcoxon rank-sum tests comparing individual perch height means between islands showed no distinction during Pre-removal ($W=179$, $p>0.7$) or Post-removal ($W=168$, $p>0.2$), but during Delayed-post removal, individuals on the one-species island perched lower than individuals on the two-species island ($W=27$, $p<0.001$).

Population perch height variance decreased sharply on the two-species island during Delayed post-removal, as this population ceased perching near the ground (Figure 4.2A, Table 4.3). However, this between-island divergence in variance was not accompanied by divergence in individual perch height specialization (as indicated by the within individual contribution to perch height variation [WIC] divided by the total niche width [TNW]; final row of Table 4.4). In other words, even though total niche width on the one-species island was twice that on the control island, the proportion of perch height variation nested within individuals, compared to the variation between individuals, was similar between islands during this final stage (0.74 vs 0.69, a difference easily explained by sampling error; see Supplemental Methods). In general, individual perch height specialization exhibited no obvious relationship to total perch height niche width throughout the experiment (Table 4.4).

Table 4.3 Comparison of population perch height variances among all island-stage combinations. Cell values represent the difference in variance (top minus left) estimated from a Tukey post-hoc test, for which the ANOVA was conducted on perch height residuals rather than raw perch height. Bold values represent differences that are significant after accounting for the family-wise error rate (i.e. p-values are adjusted for multiple comparisons).

		Pre-removal		Post-removal		Delayed post-removal	
		One-species Island	Two-species island	One-species Island	Two-species island	One-species Island	Two-species island
Pre-removal	One-species Island	-	1.6	-9.7	-8.0	0.8	-33.1**
	Two-species island	-	-	-11.3	-9.7	-0.8	-34.7***
Post-removal	One-species Island	-	-	-	1.6	10.5	-23.4*
	Two-species island	-	-	-	-	8.8	-25.0*
Delayed post-removal	One-species Island	-	-	-	-	-	-33.9***
	Two-species island	-	-	-	-	-	-

Adjusted p-value: <.05*, <.01**, <.001***

Table 4.4 Individual perch height specialization across islands and stages, as measured by within-individual contribution to perch height variation (WIC) divided by the total niche width (TNW). These values were calculated using the *RInSp* package in R, with the contribution of each individual lizard weighted by its number of observations.

	Two-species Island			One-species Island		
	WIC	TNW	WIC/TNW	WIC	TNW	WIC/TNW
Pre-removal	7570	13625	0.56	8174	13602	0.60
Post-removal	9978	11602	0.86	6409	9851	0.65
Delayed post-removal	4489	6485	0.69	9510	12784	0.74

Testing for correlated changes along other niche axes

Perch diameter

The substantial perch height changes that occurred during Delayed post-removal were accompanied by changes in perch diameter; population perch diameter mean and variance were both higher on the one-species island than on the two-species island during this final stage (Figure 4.2D, Table 4.5, Table 4.6). This between-island divergence during Delayed post-removal was driven mostly by changes that occurred over time on the two-species island (Figure 4.2D). Although mean perch diameter fluctuated dramatically for some long-lived individuals on the one-species island, the population-level distribution of perch diameters on this island was relatively stable over time (Figure 4.2E). In contrast, during Delayed post-removal, two-species island lizards occupied a narrower range of narrower perches than they had occupied during either the Pre-removal or Post-removal stages. There are also hints of an inverse relationship between individual mean perch height shift and individual mean perch diameter shift from Pre-removal to Post-removal, though the strength of this relationship is marginal at best (Figure 4.2F).

Wilcoxon rank-sum tests comparing individual perch diameter means between islands showed no distinction during Pre-removal ($W=134$, $p>0.3$) or Post-removal ($W=86$, $p>0.09$), but during Delayed-post removal, individuals on the one-species island occupied wider perches than individuals on the two-species island ($W=265$, $p<0.01$). As was true for perch height, between-island divergence in Delayed post-removal perch diameter occurred among both old and new individuals. Differences in individual perch diameter specialization between islands and across stages were negligible and could all be explained by sampling error (Appendix 2).

Table 4.5 Mixed effects model testing for population-level perch diameter shifts. Pre-removal stage lizards on the one-species island are the baseline (intercept) of this model. 'Estimated within-island change from previous stage' and 'Estimated difference between islands' are calculated by comparing the relevant coefficients estimated by the model.

		Value	Std. Err.	t-value	p-value	Estimated within-island change from previous stage	Estimated difference between islands (one-species minus two- species)
Pre- removal	(Intercept) One-species island	4.5	0.52	8.65	< 0.001	NA	-1.27
	Two-species island	1.27	0.76	1.66	0.1	NA	
Post- removal	One-species island	-0.87	0.59	-1.48	0.14	-0.87	-2.47
	Two-species island	1.6	0.73	2.18	0.03	0.33	
Delayed post- removal	One-species island	0.47	0.61	0.77	0.44	1.34	2.39
	Two-species island	-1.92	0.84	-2.28	0.02	-3.52	
Individual ID (Random effect) Standard Deviation: Intercept = 1.25, Residual = 4.80							

Table 4.6 Comparison of population perch diameter variances among all island-stage combinations. Cell values represent the difference in variance (top minus left) estimated from a Tukey post-hoc test, for which the ANOVA was conducted on perch diameter residuals rather than raw perch diameter. Bold values represent differences that are significant after accounting for the family-wise error rate (i.e. p-values are adjusted for multiple comparisons).

		Pre-removal		Post-removal		Delayed post-removal	
		One-species Island	Two-species island	One-species Island	Two-species island	One-species Island	Two-species island
Pre-removal	One-species Island	-	1.1	-0.5	1.2*	0.3	-1.8**
	Two-species island	-	-	-1.5**	0.2	-0.7	-2.8***
Post-removal	One-species Island	-	-	-	1.7***	0.8	-1.3
	Two-species island	-	-	-	-	-0.9	-3.0***
Delayed post-removal	One-species Island	-	-	-	-	-	-2.1***
	Two-species island	-	-	-	-	-	-

Adjusted p-value: <.05*, <.01**, <.001***

Lateral movement

There is no evidence that perch height changes were accompanied by changes in the extent of individuals' lateral movement. Coincident with their increase in perch height, individuals on the two-species island appear to have shrunk their lateral movement during Delayed-post removal, while lateral movement on the one-species island remained relatively stable throughout the experiment (Figure 4.2G). However, because the lateral movement metric scales positively with number of observations (Appendix 2), and individuals on the two-species island were observed far less frequently than removal island individuals during the final stage (77 observations versus 187 observations), this visual pattern

may be a result of sampling differences. Moreover, Wilcoxon rank-sum tests comparing the extent of individuals' lateral movement between islands showed no distinction during Pre-removal ($W=144$, $p>0.4$), Post-removal ($W=95$, $p>0.17$), or Delayed post-removal ($W=223$, $p>0.16$). When comparing individuals from Pre-removal to Post-removal, shifts in their extent of lateral movement were uncorrelated with shifts in their mean perch height (Figure 4.2H).

4.5 Discussion

In this study, we set up experimental conditions for ecological release of the lizard *Anolis carolinensis* from constraining interactions with its congener, *A. sagrei*, by constituting populations of lizards on small dredge-spoil islands that served as experimental units. We monitored individual and population habitat use along three niche axes (perch height, perch diameter, and lateral movement) on one experimental (one-species) island and one control (two-species) island, for three time periods: Pre-removal, Post-removal, and Delayed post-removal.

The foremost takeaway of this study is that, in this system of green and brown anoles, population-level niche changes can occur within individual lifetimes, but are not instantaneous. We saw no shifts in mean perch height until the delayed post-removal period, seven months after the removal of brown anoles from the experimental islands. This contrasts with other experimental assessments of ecological release (e.g. Bolnick et al., 2010), where both population- and individual-level niche shifts were seen within weeks. Myriad factors—the type of organism, the types of constraining interactions, and the specific niche axes under examination—may affect the dynamics of ecological release, and so, to the extent possible, experiments should persist and be monitored as long as possible to reveal longer term temporal dynamics.

Changes in perch height with time were apparent on both one- and two-species islands, indicating that despite a long history of sympatry between green and brown anoles on the source

islands from which the lizards were collected (at least 25 generations; Campbell, 2000), their introduction to our experimental islands was akin to reassembling the community. By the time of Delayed post-removal sampling, green anoles on the one-species island had moved downward, consistent with ecological release, whereas green anoles on the two-species island had moved upwards, consistent with character displacement (Stuart et al., 2014). Although ecological release and character displacement need not have strictly inverse effects on a species' niche (Herrmann et al., 2021), in this system, the processes may be like two sides of the same coin.

Nonetheless, we were surprised by the magnitude of increase in perch height with time on the two-species island—it was comparable to the increases experienced by allopatric green anoles responding to the introduction of brown anoles (Stuart et al., 2014; Kamath et al., 2020). Seasonal variation in perching behavior may have contributed to this height increase, but the limited available data suggest that seasonal shifts in green anole perch height pale in comparison to what we observed (Jenssen et al. 1995). More likely, this perch height increase was caused by brown anoles. Despite our attempt to begin the experiment with a high density of brown anoles to ensure a strong interspecific interaction, the abundance of brown anoles on the two-species island increased by nearly 50% between the Post-removal and Delayed post-removal stages as a result of reproduction (see Table 4.1 above). A recent comparison of anole communities on other Floridian islands found that green anole perch height is positively correlated with brown anole density (Kamath et al., 2020), suggesting that the green anole perch changes on our two-species island were driven by pressure from a growing population of brown anoles. In future work, setting up replicate islands in both the one-species and two-species categories will reveal if such density increases are the exception or the norm.

We are confident the perch height shifts we observed in green anoles are attributable to changes in brown anole abundance, and not some other factor. Vegetation structure was extremely similar between the islands and essentially unchanged throughout the experiment (no trees fell or lost

major limbs), so green anole niche shifts through time were not due to changes in habitat availability. Furthermore, the proximity of the islands suggests they experience comparable predation pressure from wading birds, and we observed no terrestrial predators (e.g. snakes, carnivorous mammals) on either island. Additionally, we used operative temperature models to confirm that the islands had nearly identical thermal environments during each stage of the experiment (Appendix 2). Nonetheless, we recognize that our study lacks replication in island-wide treatments (one-species versus two-species). Though this shortcoming prevents us from drawing generalizable conclusions about how ecological release unfolds, our results offer insights into the early stages of the process, specifically temporal dynamics extending into a second generation, interplay between individual and population level variation, and interactions among niche axes.

In the Delayed post-removal stage, both long-lived individuals and the young of the year perched lower on the one-species island and higher on the two-species island. The long-lived individuals' habitat use constitutes evidence against this behavior being genetically determined, and demonstrates the importance of behavioral flexibility in eco-evolutionary interactions. In this system, the morphological traits associated with perch height (toepad area and number of adhesive toepad scales) are known to evolve following changes in interspecific interactions, and include a heritable component (Stuart et al., 2014), a potential example of behavioral flexibility acting as a 'motor' for evolutionary change (Muñoz and Losos, 2018). Similar habitat use behavior by the young of the year may arise from comparable individual responses to interspecific interactions, but may also be due to social learning (i.e. copying the habitat use behavior of conspecifics; Whiting et al., 2018), which is known to be more common in young individuals in some species of lizard (Noble et al., 2014).

Despite a large niche width contraction (i.e. decrease in perch height and diameter variances) on the two-species island at the Delayed post-removal stage, we saw no change at all in the degree of niche overlap among individuals making up that population. Moreover, there were no detectable differences

in intraspecific niche overlap between islands at the end of the experiment, even though the one-species island had substantially larger population niche widths. In other words, differences in population niche width due to an interspecific interaction were driven jointly by niche changes that occurred within individuals and between individuals. These results run counter to Van Valen's (1965) Niche Variation Hypothesis (NVH), which posits that populations with wider niches due to ecological release are more likely to be made up of individual specialists than of individual generalists. Empirical evidence thus far has revealed mixed support for the NVH (Bolnick et al., 2007; Cloyd and Eason, 2016; Sjödin et al., 2018), suggesting a need for further empirical evaluations in a diversity of systems and on a variety of resource use traits.

Finally, while our results are consistent with perch height being the primary niche axis affected by interactions between green and brown anoles (Collette 1961; Stuart et al. 2014), other niche axes varied in their responses; correlated changes occurred in perch diameter, but not in the extent of individuals' lateral movement. However, the effects of ecological release we observed on niche axes other than perch height may differ across environmental contexts. For example, a correlation between perch height and perch diameter depends on the structure of available habitat (here, vegetation). Also, because researchers' ability to detect changes in animal movement depends on both the spatial and temporal extent of sampling (Kamath and Losos 2017b), we cannot rule that ecological release would alter the lateral movement of green anoles on larger islands over longer time periods. As there is no single eco-evolutionary pathway for ecological release (Herrmann et al. 2021), we should continue to study this process both across systems and across environmental conditions within systems.

4.6 Acknowledgements

This work would not have been possible without the logistical and intellectual support provided by Irene Arpayoglou and staff at the Florida Department of Environmental Protection's Aquatic Preserve Program. We thank Alexandra Bachorik, Chelsea DeCambre, Jeremy Herrmann, Ron Herrmann, Frank

Kahoun, Aaron Hochberg, and Kim Vasquez for help in the field. We also thank Debbie and Kenny Langley for additional logistical support.

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Conclusion

What happens to the residents of an ecological community when species are added or subtracted? For the green anole in southern Florida, both the addition and subtraction of a competitor, the brown anole, cause it to alter its habitat use. These niche shifts can have evolutionary consequences. Here, colleagues and I have probed competition-induced niche shifts and, to a lesser extent, their effects on morphological traits in green anoles. In doing so, we hope our readers will appreciate that processes thought to generate patterns of trait diversity in nature, including ecological character displacement and ecological release, can sometimes be observed directly in the field. Such direct observations, whether made possible by experimental manipulation or by chance events, are a necessary complement to theoretical studies and to empirical, comparative studies which can only infer process from pattern.

Appendix 1

Summary of recent literature on “ecological release” (Table A1) and “character release” (Table A2)

Table A1: According to 105 recent studies, what is ecological release? These studies were collated using Google Scholar alerts for the phrase “ecological release” in the period 11/8/18-3/24/20. Studies received in X in the fourth column if they tested for ecological release in non-native species or described or studied ecological release in the context of anthropogenic environmental change (e.g. habitat modification, climate change, overhunting). In subsequent columns, X’s correspond to the mechanism identified as underlying ecological release and to the signals accepted as potential evidence that ecological release has occurred (of which there are sometimes zero or more than one). Studies which posited a connection between ecological release and lineage diversification but clearly did not accept the latter as direct evidence of the former are marked with an X*. This table was used to generate Figure 1 in the main text. A full list of references is available at the end of this document.

Authors	Year	Taxa/System	Related to non-native species or anthropogenic change?	Release from what?				Identifiers of Ecological Release				
				Interspecific competition	Predation or Herbivory	Competition and Predation OR "Enemies"	Other OR Could not determine	Niche expansion	Density Compensation	Morphological change	Lineage diversification	Other
Amador et al.	2019	Bats					Developmental or biomechanical constraint			X		
Andrades et al.	2019	Intertidal Rocky Reefs (multiple species)	X			X		X				
Antell et al.	2020	Brachiopods and Bivalves (multiple species)		X				X				
Antonini et al.	2019	Birds (<i>Passer domesticus</i> and <i>Turdus merula</i>)	X			X			X			
Arbuckle	2018	NA			X							

Arendt et al.	2019	Pearly-eyed thrasher (<i>Margarops fuscatus</i>)	X	X		X		
Baiser et al.	2019	NA			X		X	
Balmori-de la Puente et al.	2019	Eurasian Water Shrew (<i>Neomys fodiens niethammeri</i>)			X		X	
Bathey	2019	Anna's Hummingbird (<i>Selasphorus sasin sedentarius</i>)	X		Biotic or abiotic constraints	X	X	
Beggs et al.	2019a	Noisy Minor (<i>Manorina melanocephala</i>)	X		Biotic constraints			changes in behavior (in this case, nest predation)
Beggs et al.	2019b	Noisy Minor (<i>Manorina melanocephala</i>)	X		Intraspecific Competition			individuals move into areas formerly occupied by conspecifics
Beirne et al.	2019	"Small, non-hunted species"	X		"Large-bodied, high commercial value species"			
Bellard et al.	2019	Freshwater Lakes (multiple species)	X		X			lower extinction rate
Blokland et al.	2019	Penguins (Sphenisciformes)			Could not determine	X		X* "specialisations"
Capobianco et al.	2019	Fish (Osteoglossomorpha)		X		X		X*
Chattopadhyay et al.	2020	Lesser short-nosed fruit bat (<i>Cynopterus brachyotis</i>)			Could not determine	X	X	X*
Chen et al.	2020	Old World Tree Frogs (Rhacophoridae)			Could not determine		X	X*
Chodacki and Skipper	2019	Kingfishers (Cerylinae)		X		X		
Chomicki et al.	2019	NA			Facilitation (lack of)	X		
Clouet and Gerard	2019	Treecreepers (<i>Certhia</i> spp.)		X		X		

Colom et al.	2019	Butterflies (multiple species)			X		X		
Dahl et al.	2019	Lionfish (<i>Pterois volitans</i>)	X		X			X	
Darwell et al.	2019	Ants (<i>Pheidole</i> spp.)			X		X	X	
Davis	2019	Lionfish (<i>Pterois</i> spp.)	X		X				rate of spread of invasive species
de Andrade	2019	Lagartixas (<i>Tropidurus hispidus</i>)	X		X			X	
de Andrade et al.	2019	Lizards (Teiidae)	X		X			X	
Enquist et al.	2020	"Megabiota" (multiple species)	X		X		X	X	
Espírito-Santo et al.	2019	Amazonian killifish (<i>Anablepsoides micropus</i>)			X		X		
Evans and Kassene	2019	Termites (multiple species)	X	X				X	
Feit et al.	2020	Lizards (multiple species)	X		X			X	
Filous et al.	2019	Algae (multiple species)	X		X			X	
Fitzgerald et al.	2018	Red-bellied Woodpecker (<i>Melanerpes carolinus</i>)	X	X			X		
Friedman et al.	2019	Fish (Percomorpha)		X					X*
Fulton et al.	2019	Marine Herbivores	X		X				
Gallardo et al.	2019	Red-tailed Hawk (<i>Buteo jamaicensis jamaicensis</i>)			X		X		
Gillespie et al.	2020	NA				Lack of ecological opportunity	X		X*
Gleditsch and Sperry	2019	Birds (multiple species)	X		X				
Gómez and Pérez-Ben	2019	Frogs (Pipidae)				Could not determine	X		X*
Goswami et al.	2019	Asian Elephant (<i>Elephas maximus</i>)				"Matriarchial hierarchies"			disappearance of social structure

within a
population

Granot and Belmaker	2019	NA			Could not determine	X		
Grossnickle et al.	2019	NA			Could not determine			X
Grunert et al.	2019	Therocephalia		X			X	X
Hedeholm et al.	2019	Black Dogfish (<i>Centroscyllium fabricii</i>)	X		Intraspecific Competition			
Heyns-Veale et al.	2019	Fish (multiple species)	X	X				
Hiller et al.	2019	Arthropods (multiple clades)			Could not determine	X		X
Hirano et al.	2019	Land Snails (Cyclophoroidea)						X*
Huang et al.	2020	Frogs (<i>Feirana</i> spp.)		X			X	
Hubbell et al.	2020	Darters (<i>Etheostoma</i> spp.)		X			X	
Irving et al.	2018	NA	X	X			X	
Itescu	2019	NA				X		
Jackson et al.	2019	Snakes			Could not determine			X*
Jezkova	2020	Non-volant mammals (multiple species)				X		
Jones et al.	2019	Nightingale-Thrushes (<i>Catharus</i> spp.)		X		X		
Jönsson et al.	2019	Birds (Oriolidae)		X			X	
Kingsbury et al.	2020	Coral Reef Fishes (multiple species)			"limiting factors"	X	X	
Koot et al.	2020	Grasshoppers		X			X	X*
Krabbe et al.	2020	Magellanic tapaculo (<i>Scytalopus magellanicus</i>)		X		X		
Larson et al.	2020	Coyote (<i>Canis latrans</i>)	X	X				increased resource use

										specialization
Lim et al.	2019	<i>Peperomia</i> spp.			X			X		X*
Louelle	2019	NA	X		X				X	
Meester et al.	2019	NA								Could not determine X
Michalko et al.	2019	NA	X		X				X	
Modica et al.	2019	Sea Snails (Terebridae)			X			X		X*
Mogi et al.	2019	Moqsuitos (<i>Aedes</i> spp.)	X			X		X		
Montaña et al.	2020	Fish (multiple species)								"biological interactions" X
Nguyen et al.	2020	Geckos (<i>Cnemaspis</i> spp.)			X			X		
Noble et al.	2019	Silky Pocket Mouse (<i>Perognathus flavus</i>)			X			X		
Oliveira et al.	2019	Rotifer (<i>Kellicottia bostoniensis</i>)	X		X			X		
Ord et al.	2019	Gliding Dragons (Agamidae) and Flying Squirrels (Sciuridae)				X				X
Otto et al.	2020	Macaronesia (multiple clades)	X							Could not determine island biotas are "more fragile and invisable than their mainland counterparts"
Pansu et al.	2019	African Herbivores (multiple species)	X		X					
Pejchar et al.	2020	NA	X		X				X	
Pepke et al.	2019	Birds (Campephagidae)								Could not determine X
Phillips et al.	2020	Land snails (<i>Naesiotus</i> spp.)				X		X		X*
Rauhut and Pol	2019	Dinosaurs (Tetanurae)								Could not determine X homoplasy

Refsnider et al.	2019	Horned Lizards (<i>Phrynosoma hernandesi</i>)			X		X		
Rey et al.	2019	Shrews (Soricidae)		X			X		
Reynolds et al.	2020	Lizards (<i>Anolis sagrei</i>)	X	X			X		X
Ribeiro et al.	2018	Fish (Carangaria)		X			X		X*
Ribeiro et al.	2019	Kissing bug (<i>Triatoma brasiliensis</i>)			X		X		
Ring et al.	2020	Mammals (multiple species)				Could not determine	X		
Rudak et al.	2018	Annual meadow grass (<i>Poa annua</i>)	X		X		X		increased fitness of a species
Salazar et al.	2019	Lizards (<i>Anolis</i> spp.)			X		X		increased freedom for behavioral thermoregulation
Samper Carro et al.	2019	Humans			X			X	
Sample et al.	2019	Conifers (multiple species)	X	X					
Sanchez-Chardi et al.	2018	Greater white-toothed shrew (<i>Crocidura russula</i>)			X		X	X	
Sato et al.	2019	Japanese Wood Mouse (<i>Apodemus speciosus</i>)		X			X		
Schulz et al.	2019	NA	X		X				
Soultan et al.	2019	Mammals (multiple species)	X			Could not determine			
Sullivan-Stack and Menge	2020	Sea stars (<i>Leptasterias</i> sp.)			X		X	X	X
Syslo et al.	2020	Lake trout (<i>Salvelinus namaycush</i>)	X		X		X		changes in demographic rates
Talbot et al.	2019	Common Bed Bug (<i>Cimex lectularius</i>)				Could not determine			
Taverne et al.	2019	Lizards (<i>Podarcis</i> spp.)			X		X	X	X

Teixeira et al.	2020	Lizard endoparasites (multiple species)	X		X	X		
Thompson et al.	2019	Sirex woodwasp (<i>Sirex noctilio</i>)	X	X				
Velasco et al.	2019	Lizards (<i>Anolis</i> spp.)			"Constraining selective pressures"		X	
Velasco et al.	2020	Lizards (<i>Anolis</i> spp.)			Could not determine		X	
Voje	2019	Diatoms (<i>Stephanodiscus niagarae</i> / <i>yellowstonensis</i>)			Stabilizing selection	X	X	X
Wainwright et al.	2018	Collector Urchin (<i>Tripneustes gratilla</i>)			Could not determine	X		"genetic differentiation"
Wan et al.	2019	NA	X	X				
Wesselingh et al.	2019	Freshwater mussels (<i>Dreissena elata</i>)			Could not determine		X	
Wignall et al.	2020	Bees (<i>Apis mellifera</i> and <i>Bombus</i> spp.)	X				X	
Woods et al.	2018	Jamaican monkey (<i>Xenothrix</i> spp.)			Could not determine	X	X	
Yang et al.	2018	Stone Oaks (<i>Lithocarpus</i> spp.)	X				X	X
Zhu et al.	2020	Monitor lizards (Varanidae)		X			X	

Table A2: Use of “character release” has mostly stopped. Studies were collated using Google Scholar alerts for the phrase “character release” in the period 11/8/18-3/24/20. Two studies used the term to describe an increase in phenotypic variation. The other five studies used it to denote the opposite of character displacement, defining divergence in sympatry as the result of character displacement (sympatry is the derived condition) and convergence in allopatry as the result of character release (allopatry is the derived condition). This same temporal search window yielded 105 studies for “ecological release” (Table A1). A full list of references is available at the end of this document.

Authors	Year	Taxa/System	Use in text (and page)
Itescu	2019	NA	"Ecological theories (e.g. population density dynamics, character release and displacement, niche shift and expansion) and microevolutionary patterns (e.g. the island rule, the island syndrome, loss of dispersal ability, and anti-predator defense) have seldom been studied in ILS [<i>island-like systems</i>], and empirical evidence for these is sparse." (1306)
Lyman	2019	NA	"Importantly, they found they could distinguish sympatric populations of the two species with relatively high accuracy (suggesting character displacement); where discriminatory power faded was when allopatric populations were compared (suggesting character release)." (37)
Noriyuki et al.	2019	Ladybird (<i>Harmonia axyridis</i>)	"Character release theory suggests that a species is able to exploit a greater range of habitats and food sources in an area where a similar species with which it normally co-occurs is absent (Allaby 2015). A classic example of character release is the medium ground finch, <i>Geospiza fortis</i> , on the Galápagos island of Daphne Major, where the small ground finch, <i>Geospiza fuliginosa</i> , is not distributed. On this island, <i>G. fortis</i> is a dietary generalist and exhibits a phenotypic shift in beak depth (Boag & Grant 1984)." (1)
Robert et al.	2019	Birds (multiple species)	"Indeed, we find that the average species frequency ranges are broader on the tropical island compared to the tropical mainland (Figure 2). We observe the same pattern for insects, where the total frequency range is greater on the island (1.5–23 kHz) compared to the mainland (2–19 kHz), also fitting the expectations of character release driven by a relaxation of interspecific competition." (1909)
Pérez-Miranda et al.	2020	Fish (<i>Herichthys</i> spp.)	"Character displacement occurs when the populations of two recently diverged species or related species overlap after divergence, so the competition favours the development of different morphologies. On the other hand, when the same species occur in allopatric conditions, the absence of competition promotes character release, and the species could develop similar morphologies." (6)

Slavenko et al.	2020	Skinks (<i>Papuascincus</i> spp.)	"Third, lineage B, which occurs on the Huon Peninsula with no congeners, is the largest of the small-sized lineages, even when compared to its sister lineage A (Fig. 4), possibly suggestive of character release allowing lineage B to achieve a comparatively larger size (Simberloff et al., 2000)." (8)
Suzuki and Matsumoto	2020	Japanese Weasel (<i>Mustela itatsi</i>)	"Based on a theorem of character displacement and release, <i>M. itatsi</i> , the smallest member of the mainland Carnivora guild, could become larger in a smaller island or become smaller in larger island (mainland) depending on carnivoran guild composition." (38)

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Appendix 2

Supplemental methods for Chapter 4

Can individual specialization (WIC/TNW) in perch height and diameter be explained by sampling error?

Using the *WTcMC* function in the R package *RInSp* (Zaccarelli et al. 2013), we calculated individual specialization (WIC/TNW) in perch height and perch diameter separately for each island and stage. Yet these WIC/TNW values have no associated confidence intervals for determining whether individual specialization is significantly different between islands or stages. Therefore, we ran simulations to determine whether the WIC/TNW differences we observed between islands and across stages might be explained by sampling error instead of by real, underlying differences in individual specialization.

We simulated 1000 sets of perch height observations identical to our empirical data in sample size; for each of the six island-stage combinations (e.g. two-species-island during Pre-removal, one-species island during Delayed post-removal), we matched both the number of unique individuals and the number of observations per individual to our empirical sampling. We also assigned each island-stage combination its empirically observed mean. However, the simulations for all six island-stage combinations were generated from the same underlying individual specialization, near the mean WIC/TNW observed in our experiment. We used the 1000 simulations to generate null distributions for evaluating empirical pairwise WIC/TNW differences. If the empirical WIC/TNW difference for a particular pairwise island-stage comparison fell within the middle 95% of simulated values, we could not rule out that this empirical difference was generated by sampling error. We repeated this process for perch diameter.

Of all the WIC/TNW differences we observed for perch height and perch diameter throughout the experiment, only one was 'significant' (in that it fell just outside the middle 95% of simulated values): the increase in perch height specialization on the two-species island from Pre-removal (0.56) to Post-removal (0.86). However, having compared pairwise WIC/TNW differences for six island-stage combinations ($6 \text{ choose } 2 = 15$) along two niche axes (perch height and diameter), we interpret the full breadth of these results as analogous to a single instance of statistical significance at $p < .05$ among 30 hypothesis tests. Thus, we conservatively conclude that all the WIC/TNW differences we observed may be explained by sampling error. All simulated data, along with the R script used to generate them, are available on GitHub (<https://github.com/NCHerrmann/EcologicalRelease/>).

Are any individual-level niche measurements (perch height mean, perch diameter mean, and the extent of lateral movement) correlated with the number of observations per sampling stage?

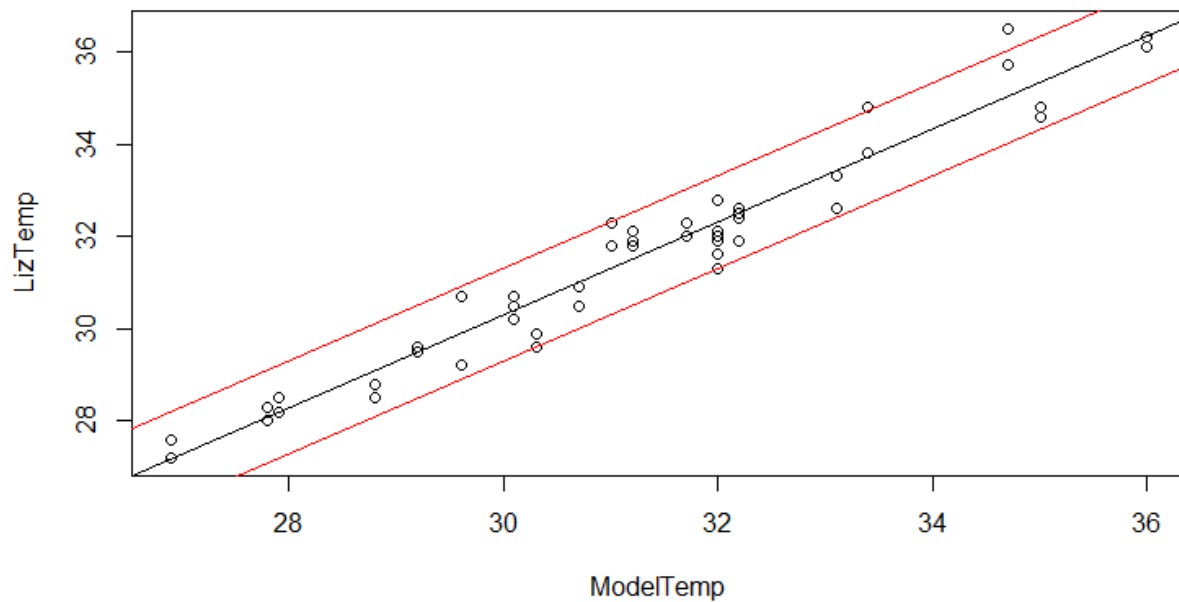
The largest individual-level niche changes along all three axes in our experiment occurred during the Delayed post-removal stage on the two-species island (SL1B). Yet this was also the population where we made the fewest observations by far (72 vs. 120-187 for the five other island-stage combinations). Therefore, we wondered whether the number of observations per individual is correlated with individual-level perch height mean, perch diameter mean, or the extent of lateral movement. If so, then perceived changes in these individual-level niche metrics may be driven by population-level sampling efforts, rather than by true changes in habitat use.

We ran a linear regression (*lm* function in R) comparing the number of observations per individual with each individual niche metric (perch height mean, perch diameter mean, and the extent of lateral movement), separately for each stage of the experiment. We find that individual perch height mean ($P > 0.6$ in all three experimental stages) and perch diameter mean ($P = .04$ for Post-removal but

$P > 0.95$ in other two stages) are largely unbiased by observation number. However, the measured extent of individual lateral movement is strongly and positively correlated with observation number during every stage of the experiment ($P < 0.001$ in stages). This correlation is the most likely explanation for the apparent decrease in lateral movement on the two-species during Delayed post-removal (Figure 4.2G in Chapter 4).

Comparing thermal environments between islands

Anoles, being ectotherms, may alter their behavior as environmental temperature changes (reviewed in Losos 2009). Seeing temperature as a possible driver of between-island differences in habitat use, we deployed operative temperature models on both islands throughout the experiment. These painted copper models were designed to mimic the thermal properties of a green anole and were field-tested the models against live green anoles to verify their accuracy (Bakken and Angilleta 2013; see Battles and Kolbe 2019 for a detailed description of model construction). The best fit line relating model temperatures (x) to live lizard temperatures (y) during field testing was $y = 1.003x + 0.183$ (black line pictured below). The red lines show, which mark plus or minus 1°C error, illustrate that almost all model readings fall within this narrow error margin.



We deployed 27 models on the one-species island (SL13C) and 28 models on the two-species island (SL1B). To ensure that models were distributed among microhabitats that green anoles might occupy, we set aside equal proportions to be placed at low (below 150 cm), medium (150-300cm), and high (>300cm) perch heights on each island. Additionally, each model was designated for placement on either the exterior (near the shoreline) or interior of each island, under the assumption that these areas might have different thermal properties. Models were randomly assigned to grid squares where they would meet their designated placement criteria (height and exterior vs. interior). Each model contained an iButton temperature loggers (Thermochron DS1921G-F5) that recorded temperature every 15 minutes.

The violin plot below shows the distribution of temperatures recorded at all models, only during the daylight hours when behavioral observations were made (7:30-18:00) and sorted by island and experimental stage. In every stage, the two islands had extremely similar thermal environments. Model

temperature means were nearly identical between islands in all stages (Pre-removal: 32.5 vs 32.9, Post-removal: 32.0 vs 32.5, Delayed post-removal: 20.7 vs 20.9). So, too, were variances (Pre-removal: 4.2 vs 4.2, Post-removal: 4.4 vs 4.6, Delayed post-removal: 3.7 vs 3.6). Environmental temperatures on both islands were clearly lower during Delayed post-removal (March 2019) than during the previous two stages (July and August 2018).

