Ecological character displacement alters the outcome of priority effects during community assembly

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Abstract. Character displacement may facilitate species coexistence through niche partitioning. However, the degree to which character displacement influences broader patterns of community assembly is unclear. Here, we capitalize on a natural experiment of community assembly on the oceanic island of Bermuda. Over the past century, three species of ecologically similar but distantly related *Anolis* lizards have been introduced to Bermuda where no *Anolis* has ever naturally existed. The Jamaican anole (*A. grahami*) arrived first in 1905 and dispersed rapidly across the island. Five decades later, the Antiguan anole (*A. leachii*) and the Barbadian anole (*A. extremus*) were introduced to independent locations. In 1991, *A. leachii* and *A. extremus* were observed to nearly meet at a contact zone, but not yet to coexist. We record that subsequent range expansion at this contact zone has been asymmetrical; *A. leachii* invaded the range of *A. extremus*, but reciprocal invasion by *A. extremus* has not occurred. When in allopatry in Bermuda, both species occupy identical ecological space. However, *A. leachii* underwent rapid ecological character displacement to use arboreal habitat when invading the range of *A. extremus*. These findings highlight how character displacement may influence the process of dispersal and drive patterns of coexistence and community assembly.

Key words: Anolis; character displacement; community assembly; introduced species; niche incumbency; priority effects.

INTRODUCTION

The processes that facilitate species coexistence and determine patterns of community assembly have been the focus of major debates throughout modern studies of ecology and evolution (Weiher and Keddy 2001, Fukami 2015, Stroud et al. 2015). Historically, community assembly dynamics have been inferred from observed patterns of species occurrences and distributions. From such observations, Diamond (1975) derived his now-classic assembly rule theory of forbidden vs. permissible species combinations, which he used to explain the observation that ecologically similar bird species rarely coexist on the same island in the Papuan archipelago. Fueled by a concurrent surge in studies of interspecific competition (Grant 1972, Case and Gilpin 1974, Diamond 1978, Grant and Abbott 1980, Schoener 1982)—believed at the time to be the principle interspecific interaction structuring ecological communities—Diamond's hypothesis spurred a series of studies exploring alternative models of community assembly that continue today (Connor and Simberloff 1979, Fox 1987, Patterson 1987, Wilson 1989, Simberloff and Boecklen 1991, Mikkelson 1993, Tilman 2004, Mittelbach and Schemske 2015). Despite decades of attention, the extent to which interspecific interactions, now recognized to also include noncompetitive interactions such as predation and mutualisms, dictate the composition of ecological communities and the distributions of species is complicated and remains unresolved. In recent years, there has been a growing appreciation that the specific order that species join a community can influence how the species in that community interact, and therefore can be instrumental in how communities assemble and the resulting final species composition (Fukami 2015). This phenomenon is known as the "priority effect" (MacArthur 1972, Morin 1999, Chase 2007; or "incumbency" sensu Fukami 2015) and parallels to its basic concept—that the order of species arrival can influence subsequent ecological patterns—have also been attributed with determining patterns of adaptive and evolutionary diversification (Rosenzweig and McCord 1991, Brockhurst et al. 2007, Fukami et al. 2007, Knope et al. 2012, Kraft et al. 2015, Brandt et al. 2016).

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The basic premise of the priority effect in community assembly is that niche space occupied by an incumbent species is inaccessible to any species that subsequently attempts to invade the community—that is, coexistence is prevented via competitive exclusion (Fig. 1b). By dictating the delineation of species' ranges through biotic interactions and niche incumbency, priority effects may therefore be important in structuring species' distributions. However, the inhibitory features of priority effects may be bypassed if ecological character displacement in one or both species occurs allowing for coexistence. In other words, niche shifts can reduce interspecific interactions that would otherwise lead to competitive exclusion, allowing the pair of formerly similar species to co-occur (Fig. 1).

Understanding how ecological character displacement can influence range dynamics is a particularly elusive aspect of ecology and biogeography (Pfennig and Pfennig 2012). Indeed, the basic premise of whether character displacement facilitates long-term species coexistence remains unresolved (Germain et al. 2017). The contemporary movement of species in response to anthropogenic activities, for example, the reorganization of communities through nonnative species introductions or climate-driven range shifts, provides many novel opportunities to test hypotheses about the processes that drive range dynamics and species distributions. Although nonnative species can have many negative—and occasionally devastating—consequences for conservation (Simberloff et al. 2013), the resultant novel communities are also valuable "natural experiments" for testing hypotheses underpinning species coexistence and community assembly (Lockwood et al. 1999, Mooney and Cleland 2001, Sax et al. 2007, Giery et al. 2013, Stuart and Losos 2013, Stuart et al. 2014, Giery et al. 2017, Kolbe et al. 2016, Stroud 2019). In this study, we capitalize on one of these natural experiments to investigate the range dynamics, assembly patterns, and ecological organization of novel communities of nonnative Caribbean *Anolis* lizards (anoles) in Bermuda.

There is a rich history of studying the ecology and evolution of character displacement in *Anolis* lizards (Schoener 1970, Losos 1990, 1994, 2009, Roughgarden 1995, Miles and Dunham 1996), including in "natural experiments" of novel communities of nonnative species (Stuart et al. 2014, Stroud 2019). Repeated bouts of ecological character displacement, leading species to adapt to new microhabitats, has been attributed as a key mechanism driving the adaptive radiation of Caribbean anoles (Williams 1972, Losos 2009). However, because of adaptive radiations being comprised of a clade of related species, it remains unclear how frequently character displacement will occur when two distantly related species come into novel contact, and if so, over what timescale character displacement will occur. For example, in anoles, the vast majority of nonnative species invasions fail if an ecologically similar anole is already established (Losos et al. 1993), providing evidence for priority effects through niche incumbency.

Bermuda is a small (53 km^2) isolated oceanic island in the western North Atlantic (~960 km east of North Carolina, USA) with only one endemic terrestrial vertebrate, the critically endangered Bermuda skink (*Plestiodon* [*Eumeces*] *longirostris*) (Wingate 1965). Over the past century, three distantly related anole species have been introduced, become established, and dispersed within Bermuda (Wingate 1965, Losos 1996; Fig. 2A–C). The Jamaican anole (*A. grahami*; Fig. 2A) was first introduced to Bermuda in 1905 and, in the absence of any congeners, quickly spread across the island. In the mid-20th century, two additional species, the Antiguan anole (*A. leachii*; Fig. 2B) and the Barbadian anole (*A. extremus*; Fig. 2C), were introduced to geographically distinct locations on Bermuda (Wingate 1965). Following successful establishment, these two species expanded their ranges toward one another's (Wingate 1965). Twenty-five years ago, in 1991, the edges of the *A. leachii* and *A. extremus* ranges were found to be in very close proximity (ca. 0.25 km apart); however, the two species were not observed to yet co-occur in sympatry (Losos 1996; Fig. 2D).
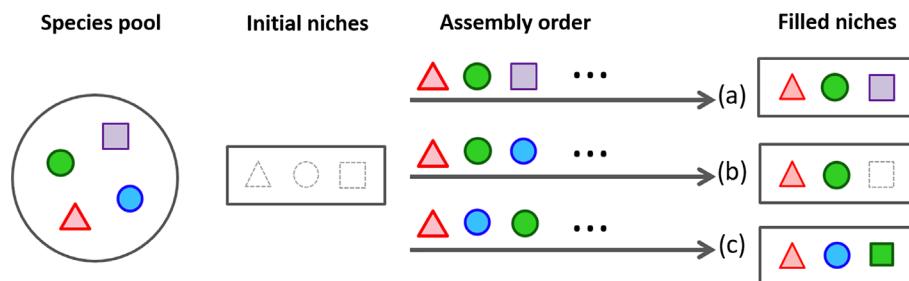

FIG. 1. Conceptual representation of mechanisms through which different ecological communities can be formed from the same species pool: (a) All species occupy independent niches. (b) An incumbent species blocks an ecologically similar species from joining the community through priority effects by niche incumbency (i.e., competitive exclusion). (c) An incumbent species blocks niche access to an ecologically similar species through priority effects, but ecological character displacement facilitates species coexistence and community assembly as each species utilizes independent ecological space. Symbol colors indicate different species. Symbol shapes denote the general ecological niche which that species occupies and dashed symbols represent vacant niches. Figure modified from Fukami (2015).

Here, we report on a recensus of species distributions in 2014 that revealed asymmetric range dynamics at the contact zone of *A. leachii* and *A. extremus*. To investigate the underlying processes driving the observed range dynamics, we returned in 2015 and conducted detailed assessments of the ecological structure and organization of all *Anolis* community types that occur in Bermuda. To characterize the structure of these communities, we quantified multiple dimensions of the species' ecologies including the use of structural habitat (i.e., perch height and diameter, two widely used metrics of ecological niche in *Anolis* lizards; Losos 2009) and diet. *Anolis* communities are most commonly structured through interspecific partitioning of these ecological axes. As

such, we expect priority effects through niche incumbency to occur when two allopatric species do not differ in any of these three ecological axes. If ecological character displacement facilitates coexistence, then we expect to see co-occurring species diverge along at least one of these ecological axes.

MATERIALS AND METHODS

Study area and history of Anolis *introductions to Bermuda*

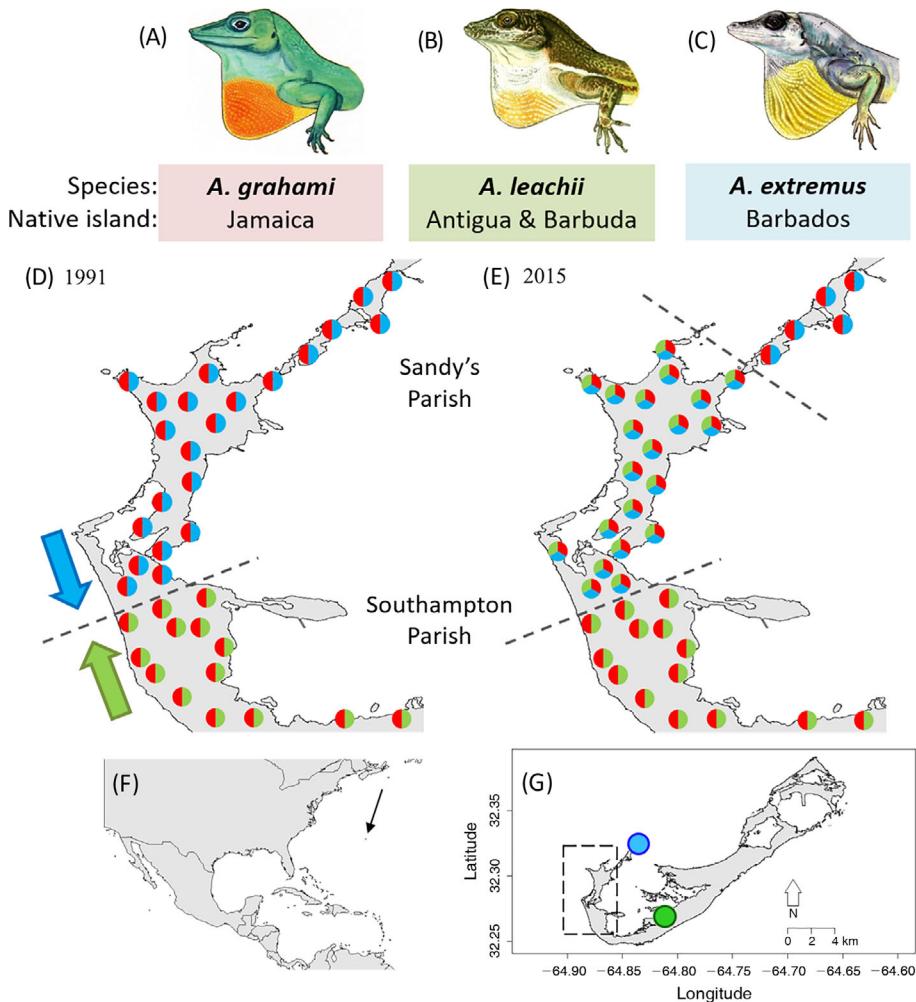The history of anole introductions on Bermuda over the past century has been well documented (Wingate

FIG. 2. Community assembly patterns at the contact zone between two species ([B] *A. leachii*; green, and [C] *A. extremus*; blue) which both underwent rapid directional dispersal from original geographically distinct locations on Bermuda (G). In 1964, only *A. grahami* (A; red) existed on Sandy's Parish, and was ubiquitous across the island except for the extreme northwestern tip where *A. extremus* established. By 1991, *A. extremus* had dispersed from its original site of introduction to form multiple two-species communities with *A. grahami*, and *A. leachii* had dispersed through Southampton Parish to the edge of the *A. extremus* range, creating a contact zone ([D]; dotted line, arrows represent direction of dispersal). In 2015 (E), *A. leachii* had invaded Sandy's Parish to form three species communities, but *A. extremus* had failed to invade through the original contact zone with *A. leachii* in Southampton Parish. Native islands from which each species originated are indicated under (A)–(C). The geographic location of Bermuda is shown in (F). Dashed lines represent range edges. Anole illustrations are used with permission from Schwartz and Henderson (1985).

1965, Losos 1996, Macedonia et al. 2016). The Jamaican anole (*A. grahami*) was first introduced onto the island in 1905 as a biological control of insect pests (Coccinelid beetles and parasitic Hymenoptera), which themselves were initially introduced as an attempted biological control of crop-destroying scale insects (Wingate 1965). In the absence of any other congeners, *A. grahami* rapidly spread and by 1963 it could be found everywhere on the island except the extreme north-western tip of the archipelago (Ireland Island, Sandy's Parish). This rapid dispersal was followed by the unintentional introduction of two congeners; the Antiguan anole (*A. leachii*) and the Barbadian anole (*A. extremus*). *Anolis leachii* was first recorded in central Bermuda in 1940. *Anolis extremus* was first documented in 1953 at a geographically independent location (Ireland Island, northwestern Bermuda; Fig. 2G). An island-wide census in 1963 documented that both of the more recently introduced species had spread from their original locations (Wingate 1965). It was predicted that *A. leachii* would continue to expand its range, because it appeared behaviorally dominant over *A. grahami* (Wingate 1965). The relationship between *A. extremus* and *A. grahami* was less clear—the two species had yet to come into contact, as *A. grahami* dispersed north and *A. extremus* dispersed south. In 1991, an updated island-wide survey was conducted (Losos 1996). Substantial range expansions were recorded for both *A. leachii* and *A. extremus* but the species' range edges had not yet met and therefore contact had still not been made (Losos 1996). Both *A. leachii* and *A. extremus* dispersed at relatively similar rates, ca. 0.27 km/yr (~14 km in 51 yr) and 0.21 km/yr (~7 km in 38 yr) respectively, from introduction to 1991. There are no marked differences in the environment or vegetation on either side of the recorded contact zone (Macedonia et al. 2016). A fourth species, the Cuban brown anole (*A. sagrei*) was first recorded on Bermuda in 2014 (Stroud et al. 2017), but is confined to two small, localized, and geographically independent, sites in central Bermuda, where it coexists with only *A. grahami* and *A. leachii* (Stroud et al. 2017). This current study did not use any ecological data from sites containing *A. sagrei*. Similarly, no data were collected at sites that support Bermuda skinks (*P. longirostris*). This approach is conservative, because *P. longirostris* is strictly a terrestrial leaf-litter species and thus likely has minimal interactions with more arboreal anoles (Stroud et al. 2017).

Species distributions and community structure

Presence–absence surveys were conducted to map the current ranges of *Anolis* lizards across the entirety of Bermuda in August 2014. We recorded the identity of lizards encountered at 114 sites that were each visited 1–3 times and searched for 10–30 min, or until 10+ lizards had been observed during any one sampling session (following the protocol established in Losos 1996). *Anolis* lizards are highly conspicuous and diurnal, which makes visual encounter surveys a suitable sampling technique for recording presence–absence (Losos 2009). No additional species were discovered at any sites during repeat samples, supporting our sampling efficacy at detecting all species present at a given site. Surveys were concentrated in areas near the apparent range edges to delimit distributional boundaries accurately, and in areas of previously unrecorded range expansions. Sites located at range edge boundaries were revisited in August 2015, but resulted in no additional species being recorded at any sites. Surveys were conducted at, or near, sites visited by Losos (1996) to provide accurate comparisons to previously published range distributions.

Ecological niche characterization

For each species and community type, microhabitat (perch) use data were collected at three or more sites. For each observed lizard we recorded its perch height (m) and diameter (cm). Perch height is the distance of a lizard above the ground; perch diameter is the width of the substrate on which the lizard is perched. We collected microhabitat data from all species in each of the three possible community types in the study area as detailed in Fig. 2; *grahami-leachii* (GL), *grahami-extremus* (GE), and *grahami-extremus-leachii* (GEL). We used two-way analyses of variance (ANOVAs) to test for differences in perch height and diameter between coexisting *Anolis* species. Both perch height and diameter data were log transformed to meet assumptions of normality. To test for habitat shifts of species between community types we ran linear models for each community type with more than one species. Linear models tested for differences in perch heights and diameters including site as an independent factor. The interaction between site and species was included to evaluate niche conservatism of all species among different sites. To test for shifts in perch characteristics of *A. grahami*—the most widespread species found in all community types—we used linear models with community type as the main factor and site nested within community type. Data on body temperatures of lizards were not collected in this study.

To assess diet, lizards were collected and euthanized, and stomach contents were removed by dissection. Stomach contents were analyzed under a dissection microscope (10–60× magnification; as in Giery et al. 2013 and Stroud et al. 2017). We conducted Mann–Whitney *U*-tests to test for differences in prey size between species in different communities. To calculate prey size, we measured the length (*L*) and width (*W*) of each prey item, and then estimated prey item volume (*V*) following Magnusson et al. (2003):

$$V = \frac{4}{3}\pi\left(\frac{L}{2}\right)\left(\frac{W}{2}\right)^2$$

To test for temporal niche consistency of species within each community type, we contrasted our perch

data with those collected in 1991 (Losos 1996) using z tests. Perch-use data were collected using the same methods and during the same diel and seasonal periods. To assess body size, we measured mass (to nearest 0.01 g); length of snout–vent, forelimbs, hindlimbs, forefoot, hindfoot, head, and jaw; and head width and depth (all to nearest 0.01 mm). All morphological traits were compared in a principal-components analysis, with the first PC axis explaining the most variation used to describe differences in overall body size between species. For all ecological and morphological data, sexes were pooled to encompass the entire variation within each species.

RESULTS

Species distributions and range dynamics

We recorded 2,615 *Anolis* lizards at 114 sites allowing us to create detailed maps of species distributions across Bermuda in 2014/2015, roughly 25 yr after the distribution census of Losos (1996) conducted in 1991. Surveys were focused on accurately delineating distributions at the contact zone of *A. leachii* and *A. extremus* as recorded in 1991 (Losos 1996; Fig. 2D). At this contact zone we detected asymmetric range expansion of *A. leachii* and *A. extremus* (Fig. 2E) that has led to the persistence of two-species (*grahami-leachii*) communities and the creation of novel three-species communities (*grahami-extremus-leachii*). These community assembly patterns have resulted from the invasion of *A. leachii* into *grahami-extremus* communities at multiple locations. In contrast, *A. extremus* has failed to invade any *grahami-leachii* communities or expand its distribution more than minimally in the past half century (Fig. 2D, E). The range expansion of *A. leachii* and its invasion into the remaining *grahami-extremus* communities is ongoing. We estimate the rate of dispersal of *A. leachii* through *grahami-extremus* communities to be ca. 0.06 km/yr (~1.7 km in 27 yr).

Priority effects and ecological character displacement

We recorded structural habitat use (perch height and diameter; $n = 748$ lizards; Appendix S1: Table S1) and diet ($n = 100$ lizards; $n = 1,401$ prey items). When in sympatry, coexisting species always partitioned ecological space in structural habitat use through differences in perch height (as in *grahami-extremus* communities; $F = 6.67$, $P = 0.01$) or perch diameter (as in both *grahami-extremus* [$F = 4.35$, $P = 0.03$] and *grahami-leachii* [$F = 14.81$, $P < 0.001$] communities; Fig. 3; Appendix S1: Table S2).

When in complete allopatry on Bermuda, *A. leachii* and *A. extremus* occupy the same ecological space (Table 1). Specifically, there were no significant differences in perch height ($F = 0.006$, $P = 0.939$), perch diameter use ($F = 1.67$, $P = 0.198$), or prey size

($W = 0.52$, $P = 0.451$) between *A. leachii* in communities of *grahami-leachii* and *A. extremus* in communities of *grahami-extremus*. Despite this niche overlap, *A. leachii* was able to invade communities of *grahami-extremus* (Fig. 3B). When *A. leachii* joined *grahami-extremus* communities (forming novel *grahami-extremus-leachii* communities), *A. leachii* increased in perch height ($F = 4.89$, $P = 0.028$) into niche space previously unoccupied by either *A. grahami* or *A. extremus*. Following the invasion of *A. leachii*, *A. extremus* did not subsequently diverge in any aspect of its ecology (perch height, $F = 0.18$, $P = 0.676$; perch diameter, $F = 3.65$, $P = 0.06$; prey size, $W = 55$, $P = 0.841$). The perch height of *A. extremus* in these novel *grahami-extremus-leachii* communities also continued to overlap significantly with that of *A. leachii* in *grahami-leachii* communities (perch height, $F = 1.01$, $P = 0.297$; perch diameter, $F = 0.66$, $P = 0.416$; prey size, $W = 58.5$, $P = 0.518$; Table 1). In sum, depending on the species present in a given community, intraspecific niche variation was high for *A. grahami*, intermediate for *A. leachii*, and nonexistent for *A. extremus* (see Table 2 for all pairwise analyses).

Body size

All three study species are medium-sized arboreal anoles; however, *A. leachii* are larger (mean mature body size [snout–vent length] = 8.86 cm; Appendix S1: Fig. S1 and Table S3) and heavier-bodied (mean body mass = 18.75 g) than both *A. extremus* (7.11 cm, 8.30 g) and *A. grahami* (6.42 cm, 6.88 g). These results are consistent with those of previous studies of this anole community (Macedonia and Clark 2003). All species are sexually dimorphic in size; males are larger than females, and size differences between species are consistent between sexes. Interspecific differences in body size (Appendix S1: Fig. S1) were determined from PC1 of a principal-components analysis of 10 size-related morphological traits that explained 96.7% of variation between species, with factor loadings ranging from 22% for snout–vent length to 71.1% for mass.

Temporal niche stability

To provide a test of temporal niche stability, we compared our perch data collected in 2014 and 2015 with comparable perch data from the same sites collected in 1991 (Losos 1996). There was no significant difference in perch use from 1991 vs. 2014/2015 in either *A. grahami* ($z = -1$, $P = 0.388$) or *A. leachii* ($z = 0.2$, $P = 0.873$) in *grahami-leachii* communities. Similarly, there was no significant difference in perch height of *A. extremus* ($z = 0.6$, $P = 0.532$), however, *A. grahami* perched lower ($z = -2.1$, $P = 0.04$) in sites that have transitioned from communities of *grahami-extremus* in 1991 to communities of *grahami-extremus-leachii* in 2014/2015.
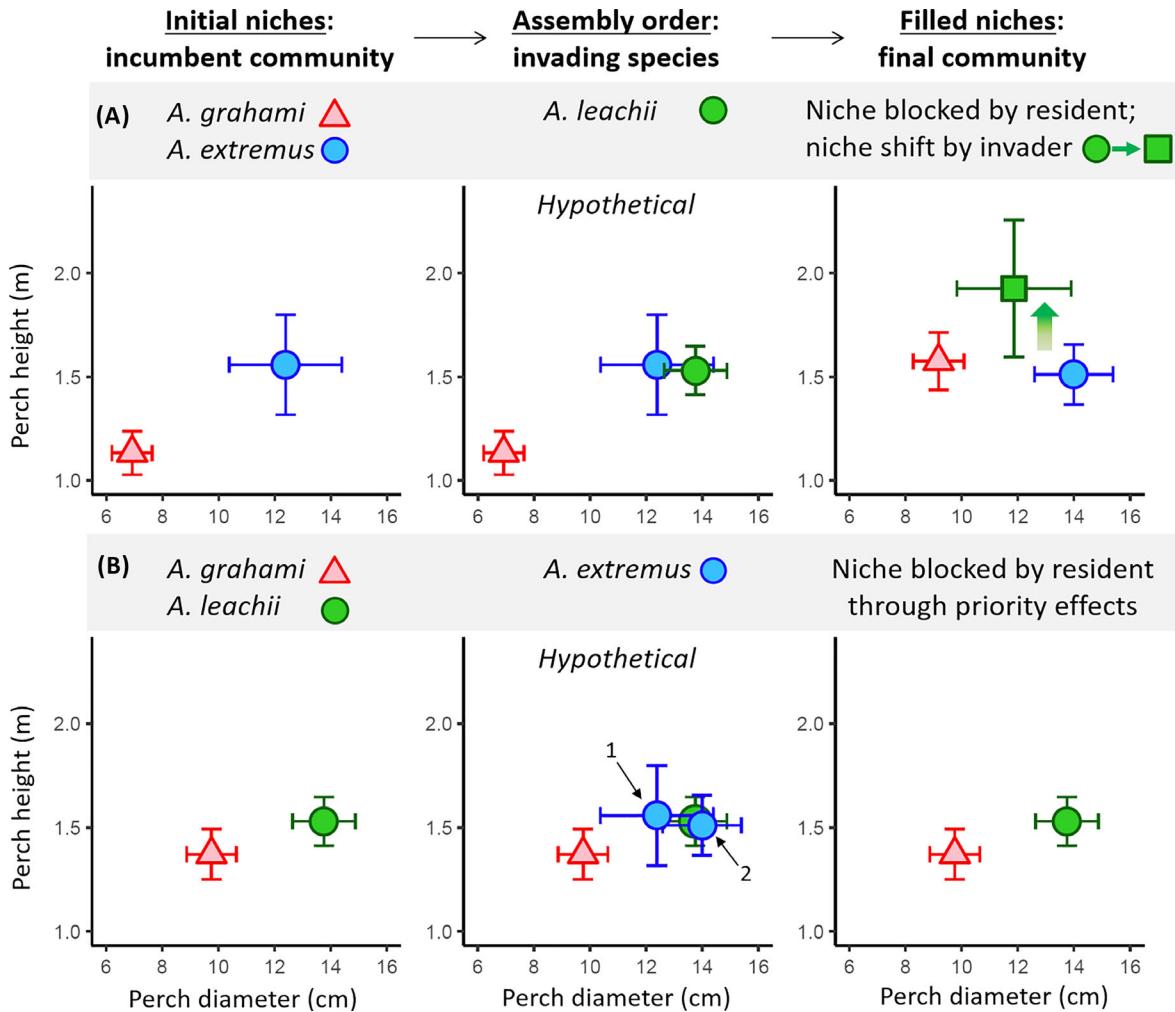
FIG. 3. Community assembly and ecological niche organization of nonnative *Anolis* lizards in Bermuda. Plots represent ecological niches of each species, here described through the axes along which divergence most commonly occurred to facilitate coexistence; structural habitat use (points represent species mean ± 1 SE). (A) *Anolis extremus* blocks ecological access to *A. leachii* attempting to join *grahami-extremus* communities through priority effects and niche incumbency. However, *A. leachii* responds by shifting its niche into unoccupied ecological space (i.e., assembly mechanism shown in Fig. 1c). (B) However, *A. extremus* is unsuccessful in invading *grahami-leachii* communities (either before [1] or after [2] the invasion of *A. leachii*) as priority effects from *A. leachii* block access to the preferred ecological space of *A. extremus* (i.e., assembly mechanism shown in Fig. 1b). The invading species (in both [A] and [B]) always significantly overlaps with the incumbent species in both axes of ecological space. As in Fig. 1, different species are denoted by colors and different niches by shapes.

DISCUSSION

In exploring the range dynamics and ecological niches of introduced *Anolis* lizards on Bermuda, we identified that rapid ecological character displacement at the expanding range edge of Antiguan anoles (*A. leachii*) facilitated invasion into a community in which its "preferred" ecological space was already occupied by Barbadian anoles (*A. extremus*). Conversely, *A. extremus* was unable to invade communities where *A. leachii* was incumbent (Fig. 3) reciprocally. *Anolis extremus* was extremely ecologically conservative through both space and time compared to *A. leachii* and *A. grahami*, both of

which responded ecologically to changes in their biotic landscapes through shifts in habitat use (Table 2). These results suggest that assembly order was important in determining final community composition ("historical contingency" *sensu* Fukami 2015) and that ecological character displacement may alter the expected outcomes of priority effects (Fig. 1).

Ecological character displacement facilitates species coexistence by promoting interspecific niche differences (Schluter 2000, Stuart and Losos 2013). In doing so, character displacement minimizes potentially costly interspecific interactions and reduces the risk of competitive exclusion. There are multiple processes that might

TABLE 1. Identifying accessible ecological space by assessing interspecific differences of invader vs. resident species of anoles on Bermuda.

Invader	Source community	Resident	Incumbent community	Priority effects?	Prey-item size		Perch height		Perch diameter	
					W	P value	F	P value	F	P value
A. leachii	GL	*A. grahami*	GE	No	72	0.2512	23.543	**<0.0001**	26.979	**<0.0001**
*A. leachii**	GL	*A. extremus*	GE	Yes	58	0.4512	0.006	0.9389	1.789	0.1828
A. extremus	GE	*A. grahami*	GL	No	115	**0.0021**	0.352	0.5537	1.502	0.2223
*A. extremus**	GE	*A. leachii*	GL	Yes	58	0.4512	0.006	0.9389	1.789	0.1828
*A. extremus**	GEL	*A. leachii*	GL	Yes	40.5	0.5183	1.126	0.2896	0.700	0.4036
A. extremus	GEL	*A. grahami*	GL	No	6	**0.0016**	0.229	0.6331	19.656	**<0.0001**
*A. leachii**	GEL	*A, extremus*	GE	Yes	81	0.3237	0.511	0.4754	1.472	0.2297
A. leachii	GEL	*A. grahami*	GE	No	92	0.5512	1.472	0.2297	16.398	**<0.0005**

Notes: Species attempting to invade a community where their preferred ecological conditions along all three niches axes are already occupied by a resident species are highlighted with an asterisk (i.e., representing priority effects through niche incumbency). Community types are as follows: *grahami-leachii* (GL), *grahami-extremus* (GE), *grahami-extremus-leachii* (GEL). Significant values are in bold.

TABLE 2. Intraspecific niche variation on three ecological axes; (1) prey-item size, (2) perch height, and (3) perch diameter.

Intraspecific niche variation			Prey-item size		Perch height		Perch diameter	
Species 1	Community 1	Community 2	W	P value	F	P value	F	P value
A. grahami	GL	GEL	9	**0.007**	3.080	0.081	1.154	0.284
A. grahami	GE	GEL	20	0.083	3.541	0.061	6.467	**0.012**
A. grahami	GL	GE	89	**0.004**	16.767	**<0.001**	1.483	0.225
A. leachii	GL	GEL	103	0.481	4.906	**0.028**	0.009	0.926
A. extremus	GE	GEL	55	0.841	0.533	0.467	3.712	0.056

Notes: Intraspecific variation was high for *A. grahami* (significant differences among all three axes), intermediate for *A. leachii* (significant difference in one axis; perch height), and nonexistent for *A. extremus* (no ecological difference between *A. extremus* and a coexisting congener). Community types are as follows: *grahami-leachii* (GL), *grahami-extremus* (GE), *grahami-extremus-leachii* (GEL). Significant values are in bold.

generate the pattern of ecological character displacement observed in this study (Stuart et al. 2017). For example, invasion by *A. leachii* into communities containing *A. extremus*, as well as the latter's ability to resist a reciprocal invasion, may have been facilitated by the larger body size of *A. leachii* and associated agonistic dominance. In *Anolis* lizards social and agonistic dominance generally scales with body size (Tokarz 1985, Losos 2009). In tandem with character displacement driven by resource competition, agonistic interactions may also drive niche divergence (Grether et al. 2009). Anoles are known to interact aggressively with co-occurring species (Jenssen et al. 1984, Hess and Losos 1991), which can drive patterns of interspecific divergence in ecology and behavior (Kamath et al. 2013, Giery and Stroud 2019). Therefore, effects of interspecific agonistic interactions may need to be considered to understand broader patterns of coexistence and community assembly.

The native range size hypothesis might explain how *A. leachii* bypassed the priority effects of *A. extremus* (Moulton and Pimm 1986, Daehler and Strong 1993). The native range size hypothesis suggests that species with larger ranges are more ecologically flexible in responding to different biotic conditions and coexisting with a larger diversity of species (Brown 1995,

Williamson 1996). However, this hypothesis cannot explain the patterns in Bermuda because the native ranges of *A. leachii* and *A. extremus* are extremely similar in size (440 km^2 [Antigua and Barbuda] vs. 431 km^2 [Barbados], respectively). An alternative explanation could be that the propensity for ecological flexibility in a given species is related to its evolutionary history of competitive interactions. In other words, species with a greater evolutionary experience of competitors may be better able to mediate novel biotic interactions through ecological character displacement. Of the three species in Bermuda, *A. extremus* originates from Barbados, where it has lived in isolation from any other *Anolis* spp. for the entirety of its existence (~6 my; Thorpe et al. 2005). A lack of interspecific interactions in its evolutionary history may explain why *A. extremus* appeared unable to change any aspect of its ecology regardless of which other species were also present (Table 2). On the other hand, *A. leachii* originates from Antigua and Barbuda, where it co-occurs with one congener, *A. wattsi*, which is both smaller and perches lower than *A. leachii* (Schoener 1970). Partitioning of perch height, whereby a larger species perches higher than a smaller species, is consistent throughout two-species *Anolis* communities of the southern islands of the Lesser Antilles (Schoener

1970, Losos 1990, 1992). On these islands, divergence in perch height and body size has been attributed to in situ character displacement (Schoener 1970, Losos 1990, 1992). On islands where only one species is present, such as *A. extremus* on Barbados, the resident is medium in size and perches at an intermittent level of arboreality. Therefore, increased perch height of *A. leachii* in the presence of *A. extremus* on Bermuda may reflect its ancestral response to encountering a novel and ecologically similar congeneric. Similarly, *A. grahami* originates from a diverse native community (Jamaica; five *Anolis* spp.), and its ecology was highly labile across the different community types in which it occurred in Bermuda (Table 2).

The anole communities on Bermuda are still dynamic. Range expansion by *A. leachii* continues and we expect it to eventually invade all remaining *grahami-extremus* communities. Other studies have highlighted that during the early stages of community assembly, sometimes termed the noninteractive phase (Wilson 1969, Simberloff and Wilson 1970), more species may be supported than will persist. As population sizes increase and competition likely strengthens, competitive exclusion may occur. All of the three-species communities can be considered to be in the early stages of assembly, having been formed relatively recently (some time in the past 25 yr). It therefore is possible that these communities have not yet reached equilibrium, and that competitive exclusion may still occur. Whether species are lost, and which species are lost, remains to be seen and should be the focus of future research. Similarly, the very recent establishment of a fourth nonnative *Anolis* on Bermuda, the Cuban brown anole (*A. sagrei*), has added another species to the island (Stroud et al. 2017). Despite being a new invader (arriving in ca. 2011; T. Garner, personal communication) with populations that are geographically distant from the nearest three-species community (ca. >13 km), *A. sagrei* already coexists with two species on Bermuda (*A. grahami* and *A. leachii*) and has been known to undergo rapid range expansion elsewhere in its global nonnative range (Lee 1985, Goldberg et al. 2002). The future range dynamics of *A. sagrei* on Bermuda, and their potential effects on other members of the *Anolis* community, provide an exciting accession in this simple model system of novel community dynamics.

Although it is clear that niches may be labile in some species when experiencing novel abiotic and biotic conditions (Miner et al. 2005, Valladares 2014, Turcotte and Levine 2016), many models of community assembly still assume that species' niches are static (Broennimann et al. 2014, Tingley et al. 2014, Vannette and Fukami 2014). Our results provide valuable insight into the role that character displacement can play in community assembly dynamics. As evidence continues to build for the importance of priority effects in other subfields of ecology and evolution, particularly in understanding patterns of evolutionary and adaptive diversification (Fukami et al. 2007, De Meester et al. 2016), addressing the relationship between priority effects and character displacement will likely provide important insights beyond the realm of simple ecological community assembly.

The global redistribution of organisms in the Anthropocene has brought a diversity of species into recent novel contact. Opportunities to study community assembly from inception, a typically elusive stage in community ecology, are unparalleled. In this study, we used long-term data on the ecology and range dynamics of introduced species across an entire island to assess the role of priority effects in the assembly of ecological communities. Without wishing to downplay the many devastating ecological consequences of nonnative species, the continued redistribution of biodiversity appears unavoidable in an increasingly connected world and will provide many valuable opportunities for future studies of community ecology (Sax et al. 2007).

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