



The 'island syndrome' is an alternative state

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Abstract

Aim: In the half-century since publication of the Theory of Island Biology, ecologists have come to recognize the importance of predation as a decisive determinant of alternate states in many ecosystems. Island species are notorious for their vulnerability to introduced predators, yet the strength of island predator regimes has not been fully incorporated into our understanding of the forces that structure island consumer communities.

Location: The Greater and Lesser Antilles.

Taxon: Birds and *Anolis* lizards.

Methods: Field surveys of sclerophyll and rainforest sites on islands ranging in size from 3.5 km² Terre-de-Haut to 76,000 km² Hispaniola.

Results: Evidence gathered in the 1970s and 1980s shows that Antillean anoles live at higher densities on fewer resources, grow more slowly, reproduce later and live longer than mainland counterparts in conformity with the 'island syndrome'. Data from this period show that Antillean bird communities display density overcompensation, community saturation, size-structured foraging guilds, low species diversity and low species packing, all traits consistent with the island syndrome and a regime of low predation and intense competition. Mainland species and communities display none of these features.

Main conclusions: I propose that the island syndrome is an alternative state that distinguishes low-predation island communities from high-predation mainland counterparts. It follows that strong mainland predation regimes tend to prevent island species from colonizing. Conversely, invasion-resistant, size-structured island communities, despite low species diversity, prevent mainland species from colonizing islands. These predictions are experimentally testable with *Anolis* lizards and, if confirmed, could set island biogeography on a new course.

KEYWORDS

birds, body mass ratios, community saturation, competitive release, density overcompensation, island biogeography, lizards, predation, supertramps

I was at Princeton University when I participated in the fieldwork.

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1 | INTRODUCTION

The last 40 years have seen a transformation in how ecologists view communities, thanks to the rise of trophic cascade theory and the associated awareness that communities can be subject to regime shifts, alternative states, hysteresis and related alterations in structure and composition (Scheffer & Carpenter, 2003). Predation is a powerful force, capable of driving regime shifts in many ecosystems (Carpenter et al., 2001; Estes et al., 2011). My purpose here is to re-evaluate some results obtained by John Faaborg and me in the 1970s in light of these recent advances. John and I made a number of trips to the Antilles between 1968 and the late 1970s, both together and separately. Collectively, we surveyed one or more sites on 16 islands, ranging from 3.5 km² Terre de Haut to 76,000 km² Hispaniola. At the time we published our results, we lacked today's comprehension of how variation in the strength of predation can drive communities into alternative states (Pace et al., 1999). Viewed through the lens of modern trophic theory (Estes et al., 2011; Scheffer & Carpenter, 2003), our results from the 1970s can now be interpreted with some confidence and fit into a coherent theoretical framework that offers critical predictions susceptible to empirical test.

I shall begin by revisiting the phenomenon of density overcompensation, a finding I regard as key to everything that follows (details below). Density overcompensation refers to higher levels of abundance of a taxonomic group or guild of species on islands than in corresponding habitat on the nearby mainland. Initially described as a response of birds to insularity, it was later documented for lizards and small mammals as well (Table 1). Why islands should support higher densities of birds or lizards than mainlands was not obvious, and various authors proposed at least three plausible hypotheses: release from competition, release from predation and release from maladaptive gene flow. Emlen's (1977, 1979) gene flow hypothesis pertained specifically to the Florida and Baja California peninsulas, which served as the mainland reference regions to islands in the Bahamas and Gulf of California, respectively. Both of these peninsulas encompass an extended latitudinal gradient, opening the possibility of genetic swamping from the continental landmass to the north

(Case & Taper, 2000). However, the remaining eight cases listed in the table were not referenced to mainland peninsulas, demonstrating that density overcompensation is not linked to gene flow in the way Emlen imagined. Distinguishing the release from competition and the release from predation hypotheses required details of demography and resource levels that were not available at the time most of these reports were published.

Resolution was achieved in an outstanding dissertation by Andrews (1979) based on a controlled comparison of anole populations in cacao plantations on Dominica, the most ecologically intact island of the Lesser Antilles, and the Costa Rican mainland. Anoles on Dominica sustained a 10-fold greater live weight on one-third the dry mass of arthropods as at the Costa Rica site, while growing more slowly, living longer and reproducing at a lower rate. In contrast, mainland Anoles grew faster, matured younger, achieved higher rates of reproduction and died sooner (Andrews, 1979). These results pointed to release from mainland predation as the principal factor in high insular anole densities. Further research has amply reinforced Andrews' findings and two recent meta-analyses have established density overcompensation in lizards as a global phenomenon, with mean insular population densities exceeding those of mainlands by an astonishing factor of 10 (Buckley & Jetz, 2007; Novosolov et al., 2016).

Recognition of recurrent patterns of demography, life history, morphology and behaviour in island versus mainland rodent populations led Adler and Levins (1994) to propose the 'island syndrome'. Synthesizing a large literature, they concluded that island mammals (predominantly rodents) live in more stable populations at higher densities, develop more slowly, mature later, reproduce less, grow larger, disperse less and are less wary and less aggressive than mainland counterparts, often of the same species. Although they did not cite her work, Andrews (1979) found that island anoles similarly grow slowly, mature later, reproduce less and live longer than mainland counterparts, affirming that the island syndrome was not restricted to mammals, as is now widely recognized (Baeckens & Van Damme, 2020; Novosolov et al., 2013).

Evidence supporting birds as also being subject to the island syndrome has lagged behind that derived from lizards and small mammals,

TABLE 1 Early reports of density overcompensation in island birds and lizards. Authors of entries in normal type favoured resource-based interpretations; authors of entries in italics favoured lower predation rates on islands; authors of entries in boldface favoured explanations based on maladaptive effects of gene flow

Author(s)	Reference	Island(s)	Mainland
Crowell (1962)	<i>Ecology</i> 43:75–88	Bermuda	Eastern U.S.
Grant (1966)	<i>Canadian J. Zool.</i> 44:391–399	<i>Tres Marias</i>	<i>W. Mexico</i>
MacArthur et al. (1972)	<i>Ecology</i> 53:330–342	Pearl Islands	Panama
Diamond (1974)	<i>Science</i> 184:803–806	SW Pacific	New Guinea
Yeaton and Cody (1974)	<i>Theoret. Pop. Biol.</i> 5:42–58	Puget Sound, WA	Mainland WA
Case (1975)	<i>Ecology</i> 56:3–18.	<i>Gulf of California</i>	<i>México</i>
Cox and Ricklefs (1977)	<i>Oikos</i> 28:113–122	Antilles	Panama
Emlen (1977)	Orn. Monogr. No. 24:1–129	Bahamas	S. Florida
Andrews (1979)	<i>Breviora</i> #454:1–51	<i>Dominica, WI</i>	<i>Costa Rica</i>
Emlen (1979)	Auk 96:152–167	Gulf of California	BC, México

presumably because birds are not readily amenable to experimentation or demographic analysis. Nevertheless, comparative studies of island versus mainland birds have upheld expectations of the island syndrome. In a global meta-analysis, island birds have been found to show increased bi-parental care and cooperative breeding, reduced fecundity, larger egg mass, longer development times and increased investment in young, all traits consistent with the island syndrome and expected in K-selected populations (Covas, 2012). Consistent with the island syndrome, Beauchamp (2021) has reported a global meta-analysis concluding that avian survival is substantially higher on islands, after removing the effects of confounding variables: latitude, body mass, clutch size and breeding system. As for behavioural adjustments, the tendency of birds to form mixed flocks is diminished on islands (Beauchamp, 2004), and may be non-existent on islands completely lacking in predators (Willis, 1972).

Consistent contrasts between island and mainland communities in so many traits, ecological morphological and behavioural, encapsulated in the concept of the island syndrome invites the conclusion that the ecosystems of many islands may exist in alternative states vis a vis continental mainlands.

Specifically, weak predation regimes allow Antillean communities of lizards, and here I'm assuming birds as well, to achieve high densities near carrying capacity. High densities, in turn, amplify both intraspecific and interspecific competition, manifested by birds as community/guild saturation, Hutchinsonian body mass ratios between successive guild members, and low species packing. All these features of the data (to be reviewed below) fit a coherent picture in which island birds and anoles are K-selected and live under conditions of low predation and consequent intense competition. Mainland counterparts, on the other hand, are r-selected and under relatively intense predator pressure that reduces population densities below carrying capacity, relaxing competition and allowing greater niche overlap, greater guild packing and higher species diversity (Martin, 1988; Terborgh, 2015). Roughgarden and Feldman (1975, p. 489) realized this long ago, stating that 'if predation pressure is strong enough there is no limiting similarity among prey; i.e., complete niche overlap should be possible'.

Accordingly, I am proposing that Antillean and mainland bird and anole communities exist in alternative states regulated, respectively, by bottom-up and top-down forces. These conclusions carry the further implication that low island species numbers result more from invasion-resistant communities structured by competition rather than by isolation and low rates of dispersal (Case, 1990; Helmus et al., 2014). Next, I shall examine some of the evidence that led me to the conclusion that the island syndrome describes an alternative state.

2 | EVIDENCE

2.1 | Community saturation

Community saturation, as defined here, refers to the observation that community-level species numbers within defined habitats increase strongly with island size and faunal richness up to islands of

a certain size and species richness but not on larger, more speciose, islands. Species numbers in the Antilles, as Faaborg and I assessed with mist nets and through comprehensive surveys in both sclerophyll and rainforest habitats, increased from the smallest island surveyed (3.5 km² Isle de Haut) to mid-size islands in the range of 500–1500 km², but not on Puerto Rico and Hispaniola, islands one or two orders of magnitude larger and supporting whole-island species pools 2–3 times greater (Figure 1; Terborgh & Faaborg, 1980).

We could find no precedent for these results in the literature of the time (1980), and after considering four hypotheses that might possibly explain the observations, we concluded that the available evidence did not support a clear interpretation. Community saturation has received little attention in the subsequent literature and remains a contentious topic (reviewed in Srivastava, 1999).

2.2 | Size structuring of avian guilds

Two years after we published the saturation article, Faaborg (1982) published a remarkable analysis that clarified the nature of the interactions underlying community saturation. He examined the size structure of four avian foraging guilds at 15 sites on 12 islands ranging in size from 3.5 km² Terre de Haut to 76,000 km² Hispaniola. All land birds were included in the analysis except for raptorial species (hawks and owls) nightjars, woodpeckers, swifts, swallows and a few others that did not fit one of the four guilds. He discovered that avian foraging guilds in the Antilles are rigidly size-structured (Figure 2; Table 2). At the time, the issue of size-structured communities was highly contentious (Simberloff & Boecklen, 1981) so that the credibility of any claim required passing the test of a null hypothesis. This was accomplished in a follow-up article in which the data in Figure 2 were challenged with null models comprised of randomly assembled guilds from both island and mainland species pools (Case et al., 1983).

The authors concluded as follows:

Typically, the size-structure of birds on these islands cannot be attributed to chance and is consistent with the competition hypothesis outlined above. The non-random distribution of co-occurring bird species with respect to their sizes stems in part from size assortment (e.g., large species are more likely to be sympatric with small species than other large species), and in part from size adjustments, whereby the same species display different sizes on different islands depending on the sizes of other sympatric species. Two alternative explanations for these non-random results, not involving interspecific competition, are discussed and rejected on the basis of existing data.

(Case et al., 1983, p. 1073)

Size-structuring explains the saturation of avian foraging guilds, given the consistent Hutchinsonian size differences between adjacent guild

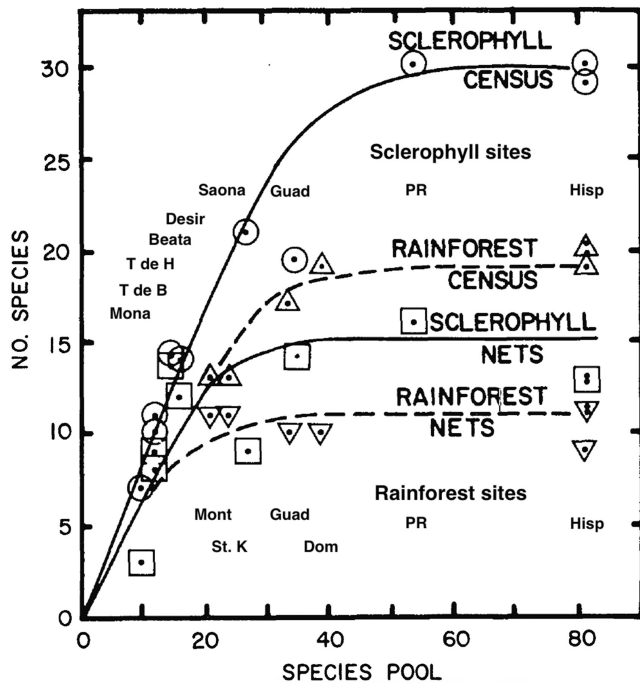


FIGURE 1 Comprehensive species counts and number of species captured in mist nest samples at 17 sites on 12 Greater and Lesser Antillean islands. Tracts of sclerophyll vegetation were surveyed on Mona, Beata, Saona, Terre de Bas, Terre de Haut, La Desirade, Guadeloupe, Puerto Rico and Hispaniola (2 sites). Rainforest habitat was surveyed on St. Kitts, Montserrat, Guadeloupe, Dominica and Hispaniola (3 sites). The abscissa represents the number of breeding land bird species on each island. Net samples are based on a standard effort of roughly 60 net-days (from Terborgh & Faaborg, 1980).

members and maximum and minimum body masses defining the size limits of guild membership. As can be seen in Figure 2, the less speciose guilds of smaller islands expand on larger islands mainly through adding species at the large or small ends of the guild size range so that guild membership expands with little reduction in the mean size ratio of adjacent guild members.

2.3 | Species packing

Comparison of species packing in equivalent Antillean and Amazonian guilds can be achieved by computing the number of guild members per doubling in body size (Table 3). Species packing in the Amazonian guilds exceeds that in the island guilds, by 2.5–7 times. Insectivorous guilds are especially crowded in Amazonia, being represented by 27 and 42 species, respectively, in the sallying and gleaning guilds versus 3 and 5.5 on large Greater Antillean islands. Regular size-structuring is not apparent in Amazonian guilds. Additional Amazonian species mostly fall within the size ranges of Antillean guilds, but species larger and, to a lesser degree, smaller, than those defining the upper and lower limits of Antillean guilds often occur (Terborgh et al., 1990).

One can argue that the contrasting island versus mainland values for species packing should not be taken at face value, for there

is a tacit underlying assumption that the respective communities are qualitatively similar. That is not the case, however, as Faaborg and I reported in Table 1 of our 1980 paper. If one puts nectarivores aside (<5% in all cases), Antillean and mainland bird communities are inverted versions of one another. Mist netted samples of birds from three Antillean islands contained 12% insectivores and 86% fruit and seed eaters, whereas two Amazonian samples contained 84% insectivores and 13% fruit and seed eaters, values similar to those from a North American locality (Maryland): 87% insectivores, 11% fruit and seed eaters. The inversion of trophic specializations in island versus mainland bird communities suggests that they are qualitatively distinct in their fundamental organization, implying that the island syndrome goes deeper than morphological and behavioural differences between species. David Lack (1976) was convinced that island ecosystems were profoundly different from mainland counterparts (his word was ‘impoverished’), but he could not say why. One reason may be that the underlying trophic systems are so different; another is that island faunas experience low predation.

2.4 | Predation

A paucity of empirical evidence on predation is the weakest element in the argument being advanced here. Predation can occur at most once in the lifetime of a prey and is thus challenging to quantify. Consequently, generations of investigators have used indirect evidence (e.g. survival rates of marked individuals, tail breaks of lizards) as surrogates for direct measurements. Annual survival of anoles on Antillean islands is high, mostly exceeding 10% and sometimes even 50% (Lister, 1981; Roughgarden, 1995; Ruibal & Philbrosian, 1974; Schoener & Schoener, 1982) whereas survival on the Neotropical mainland is characteristically low, in the range of 0.4%–9.0% (Andrews & Nichols, 1990; Paemelaere et al., 2011; Wright et al., 1984). As for Antillean birds, a single report suggests that avian survival may be modestly greater on Puerto Rico than on the North American mainland (Faaborg & Arendt, 1995). This report has recently been supported by a global meta-analysis affirming that the annual survival of birds is higher on islands than on mainlands (Beauchamp, 2021).

Birds are most vulnerable to predation as eggs or young in the nest, so it is important to consider nesting success as well as adult survival (Ricklefs & Wikelski, 2002). There are potential avian nest predators on all Antillean islands but in the absence of data, we are without means of distinguishing opportunistic predators having little demographic impact from dedicated predators having high demographic impact. Candidates include snakes (Dipsadid racers and/or boas are present on all islands in our survey; Henderson & Powell, 2009); raptors are also present on all islands (Raffaele et al., 1998); a passerine bird known occasionally to usurp nesting cavities and kill nestlings (pearly eyed thrasher, *Margarops fuscatus*) inhabits all islands surveyed but Saona and Hispaniola (Arendt, 2006); crows (two species) are confined to Hispaniola.

FIGURE 2 Dots represent the body mass in grams of guild members on each listed island: (a) sallying insectivores; (b) gleaning insectivores; (c) frugivores; (d) nectarivores. Under each guild, islands in the upper list refer to sclerophyll forest habitat, those in the lower list refer to rainforest. Islands are listed in descending order of their species pools. The few pairs of species that depart conspicuously from the pattern of wide size spacing are sufficiently different in their diet or foraging to be unlikely competitors (Faaborg, 1982, 1985). Note that the horizontal axis is scaled in powers of 2 to emphasize the evenness of the size differences between guild members (modified from Faaborg, 1982).

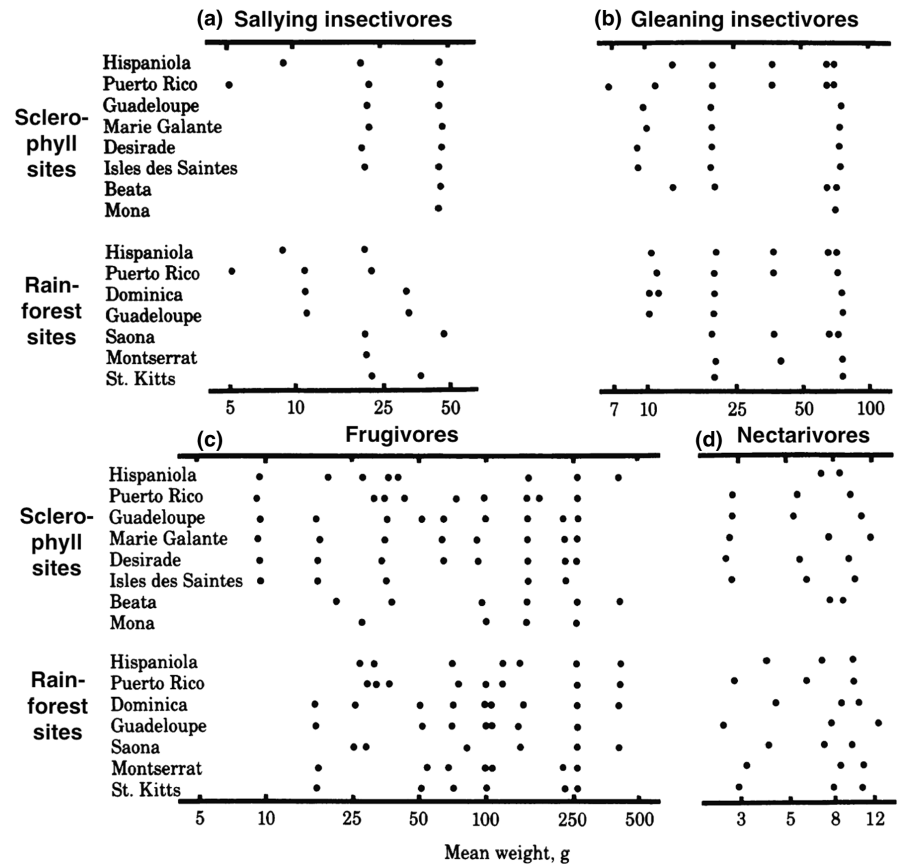


TABLE 2 Body mass ratios of adjacent guild members of four feeding guilds of Antillean birds. Number of species pairs in parentheses. Mean size ratios reported in the table are based on all pairs of species (modified from Faaborg, 1982)

Guild	Habitat	Mean size ratio \pm SD
Sallying insectivore	Sclerophyll	2.3 (8) \pm 0.44
Sallying insectivore	Rainforest	2.4 (7) \pm 0.81
Gleaning insectivore	Sclerophyll	2.0 (20) \pm 0.78
Gleaning insectivore	Rainforest	1.9 (18) \pm 0.69
Frugivore	Sclerophyll	1.8 (48) \pm 0.73
Frugivore	Rainforest	1.6 (43) \pm 0.50
Nectarivore	Sclerophyll	1.9 (13) \pm 0.36
Nectarivore	Rainforest	4.0 (14) \pm 0.69

Antillean snakes are mostly single island endemics (Henderson & Powell, 2009), so no two islands among those investigated by us support the same potential predators. Ample survivorship data indicate that anoles are under greater predation pressure on the Neotropical mainland, so one can infer that island predation regimes are weak for anoles. Predation on the nests of North American birds is strong (46% of 4208 nests monitored with remotely triggered cameras; Degregorio et al., 2016). Whether Antillean birds are subject to nest predation levels high enough to reduce interspecific competition must remain moot until the matter is investigated with modern technology.

3 | DISCUSSION

Intense research on Antillean anoles in the 1970s and 1980s generated abundant support for the view that Antillean anoles maintain higher densities on fewer resources than on the Neotropical mainland. To date, Andrews's (1979) comparison of island versus mainland anole populations appears to be the most thorough in the literature, but many independent reports provide corroborating evidence. For example, Stamps et al. (1997) found densities of female anoles on 12 Antillean islands (mean 1089 females/ha) to average five times greater than at 12 mainland sites (221 females/ha). A recent review by Novosolov et al. (2016), covering 356 lizard species found on islands and mainlands, found higher lizard densities on islands to be a global pattern.

Density overcompensation appears to be confined to island-mainland comparisons as the phenomenon has not been found in comparisons of large versus small islands within archipelagos (Terborgh et al., 1978; Wright et al., 1985), perhaps because predation regimes are more consistent within archipelagos than between islands and mainland.

The arthropod prey base of Antillean anoles, rather than being equal to or greater than that at mainland sites, as expected under the density compensation hypothesis, has repeatedly been found to be lower (Allan et al., 1973; Andrews, 1979; Emlen, 1977; Janzen, 1973). Antillean arthropods are not only less dense than mainland counterparts, but also their mean body size is smaller (Andrews, 1979). High population densities of anoles on Caribbean

Guild	Mean # spp., islands	Mass range, islands	Packing, islands	Packing, Perú	Perú/Islands
Sallying	3	5–40	0.80	5.7	7.1
Gleaning	5.5	6–80	1.46	9.6	6.6
Frugivore	8.5	9–400	1.46	5.3	3.6
Nectarivore	2.5	2.5–9.5	1.90	4.7	2.5

TABLE 3 Species packing within four avian guilds of large West Indian islands and lowland Amazonian Perú. Data for Puerto Rico and Hispaniola extracted from Faaborg (1982); values for Amazonian Perú taken from Terborgh (1980). Guild packing = (no. species in guild – 1)/log₂ (mass of heaviest/mass of lightest)

islands coupled with low prey biomass suggest that Antillean anoles are food limited, a conclusion supported by many authors (Andrews, 1976; Schoener & Schoener, 1978; Wright et al., 1984, among others).

A demonstration that mainland anoles grew faster, reproduced more and increased in density in response to supplemental feeding (Guyer, 1988) does not overturn the conclusion that mainland anoles in general live in a relatively resource-rich environment compared to Antillean counterparts. In high-predation environments, foraging entails risk, so consumers are faced with a trade-off between energy acquisition and risk of being predated (Lapiedra et al., 2018). High risk encourages minimization of foraging time. A feeding station allows an increased rate of energy acquisition, thereby lowering the time required for foraging and therefore the risk of being predated. The experiment does not address the island-mainland differences at issue here.

Community (guild) saturation is a mark of strongly interacting communities (Case, 1990; Srivastava, 1999), and should not be expected where predation moderates interactions among consumers, as on continental mainlands (Pinto-Sanchez et al., 2014). That island anole species are in strong competition with one another has been demonstrated experimentally in various contexts (Leal et al., 1998; Losos & Spiller, 1999; Pacala & Roughgarden, 1982, 1985). Similar experiments have not been performed with birds because of insurmountable logistical challenges. Therefore, affirmation of competition within avian guilds/communities can only be inferred from various lines of indirect evidence as detailed above.

Size relationships are known to be important among Lesser Antillean anoles. Islands may have either two species (one large, one small) or one species of intermediate size (Naganuma & Roughgarden, 1990; Roughgarden, 1995; Schoener, 1970; Williams, 1969). If one computes a species–area curve for Lesser Antillean anoles from data presented in Roughgarden (1995, table 2.1, p. 81), it is flat. Large islands, up to 1500 km² Guadeloupe have no more species than small islands of <10 km². The two-species islands are mostly of intermediate size. Are the one- and two-species guilds of Lesser Antillean anoles analogous to the avian guilds in Faaborg's analysis? It is an intriguing question.

3.1 | Predation

Where do Antillean birds and anoles lie on a spectrum of zero to high predation? The question has been pursued experimentally by Schoener and Schoener (1978, 1982) and McLaughlin and Roughgarden (1989)

who found that anoles survived longer on bird-poor than on bird-rich islands. Experimental introduction of a predatory lizard also resulted in reduced survival (Schoener et al., 2005). However, Calsbeek and Cox (2010) found experimentally that population density imposed stronger phenotypic selection on *Anolis sagrei* than snake predation. After reviewing stomach contents of possible avian predators of anoles on seven Lesser Antillean islands, Wright (1981, p. 199) concluded that 'avian predators are probably not a significant cause of mortality among anoles in dry, sclerophyll scrub in the Greater and Lesser Antilles'. Whether or not predation on Antillean anoles is regarded as 'significant', the data are consistent in pointing to higher levels of predation in mainland localities (Andrews & Nichols, 1990; Wright et al., 1984). A global review by Novosolov et al. (2016) concurred, finding higher lizard survival on islands without snakes, but better survival on islands with snakes than on mainlands.

Extensive monitoring of nests of North American birds with remotely triggered cameras found that 46% of nests were predated (Degregorio et al., 2016). However, out of 90 documented predators, only three accounted for more than 2% of predation events: black rat snake (*Elaphe obsoleta*, 11%), raccoon (*Procyon lotor*, 6%) and Cooper's hawk (*Accipiter cooperii*, 3%).

Whether there are dedicated predators of bird nests in the Antilles is unknown, but the circumstantial evidence is unconvincing. Raccoons and rat snakes (*Elaphe* sp.) do not occur in the Antilles and accipiters are confined to the larger Greater Antillean islands. In any case, a simple answer is unlikely because almost every island has its own endemic snake species (Henderson & Powell, 2009) and distinct avifauna (Raffaele et al., 1998). In addition, all islands have introduced rats (*Rattus rattus*) and many have mongoose (*Urva auropunctata*) as well. However, adding up the number of potential predators at a site and using the number to represent predator pressure has failed to yield positive results, either for lizards (Novosolov et al., 2016) or for nests of North American birds (Degregorio et al., 2016).

Effective predators can drive state shifts in ecosystems, as exemplified by the largemouth bass (*Micropterus salmoides*). In many North American ponds and lakes, the presence/absence of largemouth bass determines the underlying trophic structure of the ecosystem. With bass, the water body is typically clear; without them, the water is turbid with algae among many additional differences (Carpenter et al., 2001). Limnologists have made great progress in understanding the process of state shifts in lakes and streams, but terrestrial ecologists have been more reticent about using the language of alternative states to describe their results, although evidence from many types of ecosystems unequivocally shows that

alternative states occur in terrestrial ecosystems when the top trophic level is removed (Estes et al., 2011; Terborgh et al., 2001).

I have reviewed evidence pointing to the Antilles as a low predation–high competition environment for birds and anoles, notwithstanding the presence of some predators that regularly prey on lizards, or birds and likely also on the eggs and fledglings of birds. It is the effectiveness of these predators in regulating the populations of birds and anoles that is at issue. The evidence presented by Andrews (1979) and the confirmation provided by many subsequent authors decisively affirms the prevalence of low resource availability, strong competition and K-selected life-history attributes in Antillean anole populations. Although we do not have the same types of evidence for birds, density overcompensation, community saturation, Hutchinsonian size ratios and species-poor guilds found across the Antilles are all consistent with competition structured communities characterized by high population densities, high individual survivorship and low species diversity (Martin, 1988; Terborgh, 2015).

The observations reviewed here are consistent with the island syndrome and have led me to the conclusion that the predation regimes prevalent on Antillean islands of all sizes are weaker than those prevalent on the American mainland. The largemouth bass analogy is thus plausible background to concluding that Antillean and mainland bird and anole communities represent alternative states.

4 | TESTS OF THE ALTERNATIVE STATES MODEL

This is not to claim that all islands will conform to the same model. Looking broadly at island systems around the world, it is realistic to imagine that they will fall on a scale from low predation and strong competition to high predation and low competition with corresponding adjustments in the demographic and community features considered here. Working out the details and consequences of such differences could occupy future island biogeographers for a long time. Curiously, a recent essay on the opportunities for future research on island biogeography does not mention the strength of trophic interactions as a topic of interest (Warren et al., 2015).

In closing, I point to the possibility of conducting empirical tests of some conjectures that follow from the arguments presented here. If Antillean birds were found to be subject to levels of nest predation comparable to those recorded on the mainland (Degregorio et al., 2016), then the conclusions expressed here would have to be reconsidered.

Other possible tests could be designed to expose the forces that control island–mainland faunal interchange. The Antilles are annually flooded with North American migrant birds of more than 200 species, yet none of these attempts to breed in the islands (Raffaele et al., 1998). Conversely, 21 species of Bahamian/Cuban birds not recorded as breeding in the United States were observed by bird-watchers in southern Florida in a recent 2-year period (eBird, 2021). One has to presume that this level of testing the waters has been going on for thousands of years. Thus, dispersal does not appear to

be limiting colonization in either direction. Instead, the bottleneck for immigrants must be establishment. If island birds are postulated to be weak competitors, mainland immigrants should be able to invade and swamp island communities, but that does not happen. The prediction that emerges from the arguments presented here is that Antillean species are strong competitors that live in size-structured guilds capable of resisting potential invaders from the mainland as well as from within and between islands (Case, 1990). There is, however, evidence of bi-directional invasions of anole clades in deep time (Patton et al., 2021). Nevertheless, Antillean predation regimes are postulated to be weak, leading to relaxed anti-predator adaptations that leave island species vulnerable to mainland predators (Wright et al., 2016).

A related issue is the 'supertramp' phenomenon, described by Diamond (1974) as bird species confined to small islands, often situated within sight of large islands or mainlands. Diamond characterized supertramps as good dispersers but poor competitors, as evidenced by their confinement to small islands and apparent inability to invade more speciose communities. Given these circumstances, it is likely that the tiny islands to which many supertramps are confined are essentially lacking in predators. Thus, the alternative hypothesis is that supertramps and other 'low S' species are excluded by predators from larger, more speciose landmasses because they have evolved in a context in which defences against predators have not been advantageous (Wright et al., 2016). Supertramp lizards are possible under Diamond's definition, but to my knowledge none have yet been recognized.

These hypotheses can be examined using island and mainland *Anolis* lizards in controlled experiments. The practicality and success of such experiments has been repeatedly demonstrated in island versus island comparisons (Kolbe et al., 2012; Lapiedra et al., 2018; Pacala & Roughgarden, 1985; Pringle et al., 2019; Schoener et al., 2002), but to my knowledge there have been few, if any, attempts to compare island versus mainland anoles experimentally. Well-constructed experiments should be able to distinguish the competition versus predation hypotheses and support or reject the ideas presented here.

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CONFLICT OF INTEREST

The author declares no conflict of interest.

DATA AVAILABILITY STATEMENT

The data presented were taken from Terborgh (1980), Terborgh and Faaborg (1980), and Faaborg (1982, 1985), all sources available in the public domain.

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BIOSKETCH

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