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Using introduced anoles as natural experiments in ecology and evolution

My dissertation research attempted to test several fundamental ecological and evolutionary hypotheses using communities of introduced non-native *Anolis* lizards. The idea to use non-native species as 'natural experiments' in ecology and evolution certainly isn't new, in fact I can't even claim any anole-specific originality to the idea[4]. However, to my surprise, few people had so far jumped on board this train so far in Miami, FL, where I had found myself enrolled in graduate school at Florida International University. I had arrived in south Florida having accepted a PhD position in the lab of Ken Feeley – a specialist in studying how tropical plants are responding to climate change in the Peruvian Andes. The plan was for me to investigate whether the patterns Ken had uncovered in the Andes – that plant distributions were shifting upslope in response to contemporary climate change – extended to the cold-blooded (and therefore [presumably] similarly thermally sensitive) herpetological diversity. Yet, I had found myself already in a lush subtropical metropolis surrounded by lizards. I soon learned that the vast majority of this peculiar fauna were Caribbean *Anolis*, and the more I watched and read about anoles, the more they fascinated me[5].

An adult male Cuban brown anole (*Anolis sagrei*) in Miami, FL.

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[4] See the last paragraph of Chapter 11 in Jonathan's book (Losos 2009), "Finally, introduced species provide unparalleled opportunities to study ecological interactions and their evolutionary effects [in *Anolis*]", as well as all of the other [introduced] anolologists who's shoulders I have stood on.

[5] I had always come from a lizard/reptile research background; I had (partially) tricked my way in to Ken's lab under the guise of being a forest ecologist (having completed by Master's research on forestry plantations, albeit only in the context of looking for snakes within them). On reflection, there was little chance that Miami's diverse exotic lizard community wasn't going to steal my attention. Also, I learned early on that the Andes get cold. That wasn't appealing to me.

Like most anole researchers, I soon became interested in the over-arching and broad questions concerning the origins and maintenance of such diversity. Specifically, I was interested in four main topics; (i) what triggers adaptive radiations, (ii) once a clade starts to radiate, how do phenotypically-similar species coexist, (iii) how does this influence broader patterns of community assembly, and (iv) what are the ecological, behavioral, and morphological consequences of coexistence?

Much of our understanding about the mechanisms that have generated anole diversity has relied on inferring process from pattern. In some senses, this is unavoidable; evolutionary biology is classically historical in nature – one must collect evidence in the present to test hypotheses about the past (Cleland 2001, Mayr 2004). For the most part, the picture we have of anoles is already an end product; adaptive radiation has happened, and we are left to study only those species which have stood the test of time. However, what generates this diversity? How do interactions in the early stages of radiation shape patterns of diversification? How do species coexist if they have not yet diverged in phenotype? These are all fundamental yet difficult questions surrounding the (notoriously elusive) early stages of adaptive radiation. In the absence of identifying a natural scenario in which early stages of divergence could be occurring among closely-related species (these situations are often cryptic and difficult to identify[6]), observing the processes which drive early stages of divergence would be much easier with a time machine.

However, there are contemporary alternatives, which I will take this opportunity to discuss. But first, to understand how to study these processes we must first pick apart the various stages of adaptive radiation and identify the assumptions that underlie them. Here, I loosely follow the classic model of adaptive radiation as first put forward by Simpson (1953) and then developed further by Schluter (2000)[7]:

1. An ancestral species finds itself in a resource-rich environment.
2. Speciation occurs; (reproductively-isolated) species coexist and communities assemble.
3. Resources are partitioned to minimize (costly) interspecific interactions[8].
4. Species adapt to each respective 'niche'.

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[6] Although see Rich Glor, Julienne Ng, Anthony Geneva, and Dan MacGuigan's (and associated colleagues!) excellent work investigating patterns of divergence in the *distichus* complex.

[7] But which I, like many anole students, discovered by way of Losos (2009, p.206-7).

[8] Classically, interspecific exploitative competition for resources is the interaction expected to drive this process (and the most common approach taken in anoles), and so a depletion of resources leading to resource limitation would be expected priori to partitioning. However, the degree to which interference competition, for example agonistic interactions, can drive the same patterns deserves more research attention (in adaptive radiations in general, and in anoles specifically).

I will discuss each stage of this model of adaptive radiation, attempt to explain how my research has picked apart at (small) pieces of the story, and highlight opportunities which I think deserve further study.

1. *Ecological opportunity*

The initial stage of adaptive radiation in which a species finds itself with new access to competitor-free resources is usually referred to as *ecological opportunity*. Classically, ecological opportunity, like adaptive radiations themselves, is often thought about in the context of islands. For example, an ecological opportunity may be presented following the colonization of an island depauperate in competitors. Famous case studies of island radiations include Darwin's eponymous finches in the Galapagos, or the lobeliads of the Hawaiian archipelago. However, this may also span to other island-like scenarios, such as the colonization of land-locked lakes (as in the African Rift Lake cichlids or the Sulawesi silversides). There are other ways in which an ecological opportunity may be experienced: following a mass extinction (for example, the explosive radiation of mammals following the extinction of the archosaurs and other non-avian dinosaurs), the appearance of new resources (such as new habitats which developed during the uplift of the Andes), or key innovations[9] (like the evolution of the pharyngeal jaw of cichlids and the explosive diversification in trophic morphology which followed; Fig 1). As the start of my dissertation, I reviewed the relationship between ecological opportunity and adaptive radiation (Stroud & Losos 2016), although not explicitly within the context of anoles.

Luke Mahler's work had previously found macroevolutionary support for the role of ecological opportunity – as defined by rates of diversification decreasing through time (i.e. ecological opportunity was highest at the start of the radiation because trait diversification was fastest, but then decreased through time as that trait-space was filled) – in the adaptive radiations of anoles (Mahler et al. 2010). However, we know very little about how ecological opportunity works mechanistically. One way to think about ecological opportunity would be to visualize a species gaining access to a new adaptive landscape which is comprised of many unoccupied peaks (each representing a distinct ecomorphological phenotype). Through time, colonization of those peaks, with selection carving out the valleys separating them, will produce an adaptive radiation – each species in the radiation will find itself stranded on an independent adaptive peak. However, what the shape of (multi-species) adaptive landscapes actually look like, much less how natural selection acts to shape them, remains poorly understood[10]. This is true at both the

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[9] Some suggest that the evolution of toepads in anoles are one such key innovation, providing access to the arboreal realm with far greater performance than any other competitors (see Losos 2009 p.332-5 for a nice summary)

[10] A further piece to this puzzle is that, so far, estimates of fitness surfaces at the microevolutionary scale in anoles has relied on survival fitness rather than reproductive fitness. A clearer evaluation of how well these two estimates reflect true biological fitness in anoles would be valuable.

micro- and macro-evolutionary scale. Following Luke's work, little progress has been made on the role of ecological opportunity in anole radiations; a more detailed macroevolutionary understanding of how the landscape itself evolves (if it is considered to not be static through time) would help to further bridge the pattern-process divide.
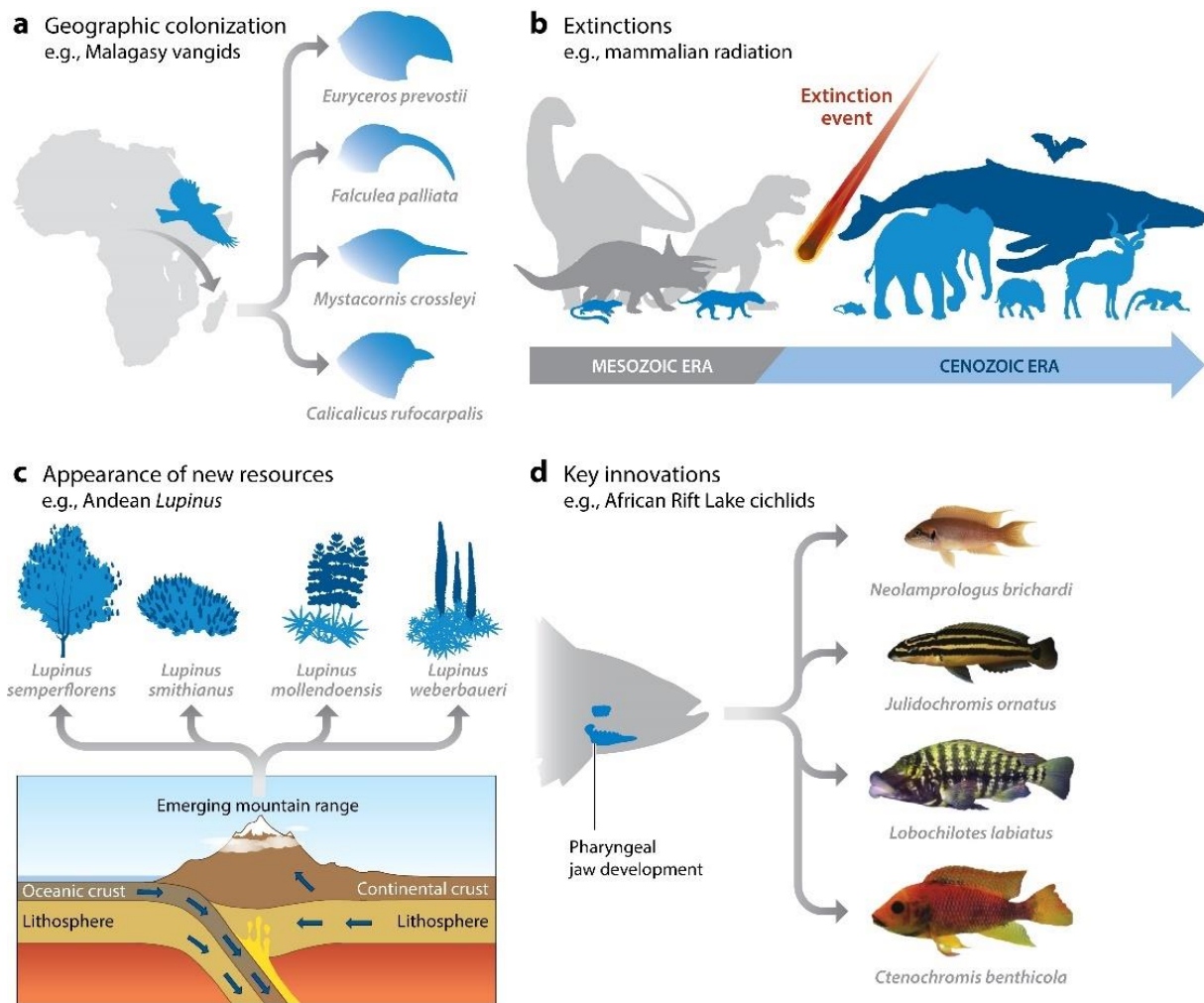
Fig 1. The various ways in which an ancestral species (or clade) may experience an ecological opportunity (from Stroud & Losos 2016, which also includes a much more informative figure legend; used with permission of *Annual Reviews*).

(1.b *Ecological release*)

Following the discovery of an ecological opportunity and free from the shackles of previous biotic constraints, an ancestral species may be expected to take full advantage of the breadth of this new and exciting resource spectrum. As the diversity in resource use of the ancestor expands, this will present as an increase in total niche width. This process of niche

expansion is known as *ecological release*. This hypothesis is of particular importance to adaptive radiations as it provides the mechanistic basis on which disruptive selection can drive within-species divergence[11]. If assortative mating occurs within these diverging phenotypes, then reproductive isolation may evolve, and lead to sympatric speciation[12]. So far, there has been very little evidence for sympatric speciation having occurred in anoles. Two lines of evidence support this; (i) a lack of gene flow (and regions of sympatry) among sister species in the Greater Antilles[13], and (ii) the two-species islands found in the Lesser Antilles would appear a likely place for it to have occurred, yet all species pairs are not closely related and are the result of independent colonization events.

The reason I discuss sympatric speciation (despite previous studies providing relatively little support for it in anoles), is that there also exists scant support for something often considered an important precursor – *ecological release* – in the anole literature[14]. If we are to fully understand whether sympatric speciation occurred in anoles (or, even, if it was *likely* to have occurred), then a better understanding of ecological release would be valuable. The current prevailing view of anole radiations is that they were largely driven by bouts of allopatric speciation with phenotypic divergence occurring on secondary contact (e.g. through character displacement) or local adaptation in allopatry. Whether ecological release existed, exists, or would be predicted to exist in anoles remains unclear and deserves further investigation[15]. Introduced species could provide a unique opportunity to study this at the ecological level; a handful of successful invaders (e.g. *A. sagrei, A. carolinensis, A. distichus,* and *A. cristatellus*) are now found in a range of different ecological communities. These communities are often comprised of many different species and so may represent a biotic gradient with which to test for the presence of ecological release through quantifications of resource use and niche breadth[16]. Alternatively, the comprehensive ecomorphological assessment of multiple island populations of

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[11] A nuance to this is that the population must have high within-population variation for disruptive selection to occur; ongoing research with Sean Giery aims to understand this pattern in a widespread focal species (*Anolis sagrei*), while work with Ambika Kamath and Michele Johnson aims to elucidate patterns of within-population variation (now fashionably referred to as 'individual specialization') across anole species and ecomorphs.

[12] This is just one mode of sympatric speciation and a highly simplified synopsis at that – see Nosil (2012) for much more detail!

[13] Ongoing work by Guinevere Wogan and Ian Wang is attempting to uncover ancient hybridization in the Puerto Rican clade, which may yet reveal new insights.

[14] Only Lister (1976) has so far provided convincing empirical support for ecological release in anoles, which stems from his ecological assessments of *A. sagrei* in various natural communities of different compositions; the so called "chronosequence" method.

[15] Ecological release may occur in the allopatric speciation model of adaptive radiation, as often favored in anoles, but it isn't thought of as a necessity in the same way as under as sympatric model of adaptive radiation.

[16] See Sean Giery's contribution in this issue which presents some of our research testing the ecological release hypothesis in *Anolis sagrei*.

the brown anole (*A. sagrei*), spanning its entire natural distribution and spearheaded by Graham Reynolds and Anthony Geneva (among others), may provide the same chronosequential comparison.

If support for ecological release is found in anoles, then the ensuing conversation about its evolutionary implications will be interesting. Presumably, if accepting that sympatric speciation is an unlikely outcome, a broader niche – in concert with high within-population variation – could pre-adapt a species for novel interspecific interactions. For example, if phenotypes already exist in a population which would be favored under novel selection regimes (for example, if interacting strongly with a novel congener), then coexistence may be achieved from rapid phenotypic shifts, side-stepping the alternative; competitive exclusion. In these ways ecological release of two species in allopatry could accentuate (and possibly accelerate) character displacement on contact, driving the rapid diversification patterns observed in anole radiations. However, if niche expansion through ecological release is driven by increased generalization of individuals (i.e. the opposite of individual specialization), then this adaptive power is presumably lower. Therefore, it is important to not only understand the basic pattern of ecological release (niche expansion), but also the underlying structure of it (degree of within-population variation; "*individual specialization*"). I aim to establish future research projects to address some of these questions.

2. *Speciation, species coexistence, and community assembly*
There is no avoiding that speciation is an integral component of adaptive radiation. However, I am not going to discuss (in more detail) the various phenomena through which speciation can take place. I will, however, take this opportunity to briefly highlight that we still know very little about assortative mating patterns in anoles; this would be a rich opportunity for future research given its apparent importance in evolutionary radiations and to the process of speciation.

Instead, I will focus this section more on the other topics at hand which comprised the majority of my dissertation research; *species coexistence* (and the phenotypic consequences of it) and *community assembly*. While these can (generally) mean the same thing depending on the scale in which they are discussed, I will refer here to *species coexistence* as investigating the coexistence mechanisms of a focal pair of species, while *community assembly* as co-occurrence patterns of more than two species. I conducted separate studies on these two phenomena during my dissertation research. To study patterns of community assembly, I travelled to the island of Bermuda, while I conducted a detailed investigation on coexistence of phenotypically similar species on two trunk-ground ecomorphs in Miami, Florida.

Bermuda has a rich and well-documented history of anole introductions spanning the past century[17]. In 1905, Graham's anoles (*A. grahami*) were purposefully introduced from Jamaica as a biological control of crop-destroying scale insects (*Carulaspos minima*) (Wingate 1965). Despite the quick establishment, high population density, and rapid expansion of *A. grahami* in Bermuda, the scale insect population did not appear to suffer. Upon analysis of the stomach contents of a selection of *A. grahami*, it was discovered that these lizards rarely – *if ever* – ate scale insects...this was the first stage of a calamitous cascade of biological invasions on Bermuda. *Anolis grahami* quickly became so abundant that in the 1950s it was deemed that their population now needed control. And so, in 1957, Great kiskadee flycatchers (*Pitangus sulphuratus*) were introduced from the Jamaican realm of *A. grahami* to control the lizard populations. As you may have predicted, in a classic case of conservation _mis_-management, kiskadees also rarely, if ever, ate *A. grahami* (Fig 2). Both species flourished and are now found across the entirety of the island.

Fig 2. A Greater Kiskadee flycatcher (*Pitangus sulphuratus*) not eating an anole.

In the 1940's two additional anoles were introduced, albeit this time unintentionally[18]: first, the Antiguan anole (*A. leachii*; known locally as "the Warwick lizard") was observed in Central Bermuda, and second, the Barbadian anole (*A. extremus*) was recorded from Sandy's Parish in north-west Bermuda. Losos (1996) conducted an update in 1991 of the distributions of each species since the last comprehensive survey 30 or so years prior (Wingate 1965). Losos (1996) observed that both *A. leachii* and *A. extremus* had dispersed towards each other, and were

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[17] And these introductions were not limited only to anoles; Bermuda is also the only place in the world (to my knowledge) where someone has attempted to introduce Galapagos marine iguanas. That credit falls to the Bermudian naturalist Louis L. Mowbray, who thought it was a good idea in 1933. Unfortunately, due to the absence of its main marine food source, none survived. His exploits with other Galapagian fauna were more successful: Mowbray was the first person to successful breed Galapagos penguins and giant tortoises in captivity, some of the latter are still housed at the Bermuda Zoo.

[18] Or at least, no evidence has surfaced so far suggesting that it was intentional, although it seems most likely.

tantalizingly close to meeting at contact zone, but had not yet done so (within 250m!). Sean Giery and I returned in 2014 and 2015 to provide the third update in this series to discover what had happened during the next 30 years[19].

We discovered that range expansion at the contact zone of *A. leachii* and *A. extremus* had been asymmetrical; *A. leachii* had invaded the range of *A. extremus*, but this was not reciprocated (Fig 3). This was a curious result, and so we set about attempting to understand the ecological and behavioral mechanisms which may have driven this pattern.
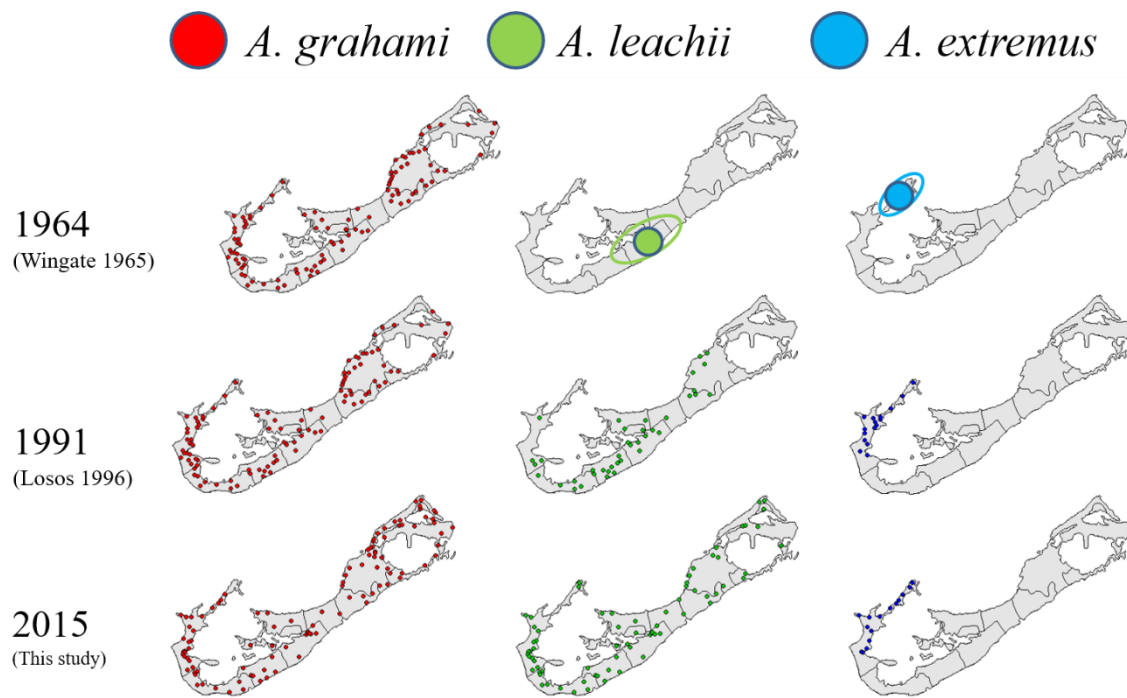
Fig 3. The range dynamics of introduced anoles on Bermuda. 1964 highlights the site of introduction (large dot) and the estimated range (ellipse); at this time *A. grahami* was already found across the island. In the ensuing years, Losos (1996) record range expansion in both *A. leachii* and *A. extremus* although the ranges had not yet met. We returned to see that range expansion at this contact zone had been asymmetrical.

Through detailed assessments of the ecology of each species, we saw that *A. leachii* and *A. extremus* were extremely ecologically similar when existing in allopatry in Bermuda (in other words, when in a community with only *A. grahami*, which is ubiquitous). They overlapped

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[19] It would be unfair to say that we were the only people aware of this; Joe Macedonia had been working in Bermuda for a number of years and was also interested in documenting the range dynamics (Macedonia et al. 2016). Joe was exceptionally helpful, welcoming, and supportive of my research studies in Bermuda.

significantly in all of the major resource axes: perch height, perch diameter, and diet[20]. However, when *A. leachii* invaded communities of *A. extremus* and *A. grahami*, it shifted dramatically (and significantly) to higher perches (and into a region of ecological space under-used by both resident species). Conversely, we observed that *A. extremus* does not change any aspect of its ecology in any community it's found in on Bermuda. These patterns provide support for two things; (i) the role of priority effects in community assembly, and (ii) that niche shifts may alter the outcome of priority effects.

We suggest that priority effects through niche incumbency is displayed by both *A. leachii* and *A. extremus*. In other words, once either spaces occupied a given niche space, it was rendered unavailable to an ecologically-similar invader. However, we observed that ecological character displacement (i.e. niche shift to increased arboreality) allowed *A. leachii* to bypass these priority effects, and therefore influence patterns of coexistence and community assembly (Fig 4; Stroud et al. 2019 [hopefully]). These points form the majority of the formal discussion that resulted from this study, but I will now take the opportunity to discuss the next obvious question from this pattern: why does *A. leachii* shift and *A. extremus* doesn't? I don't have any particularly robust answers, and so here comes some speculation.
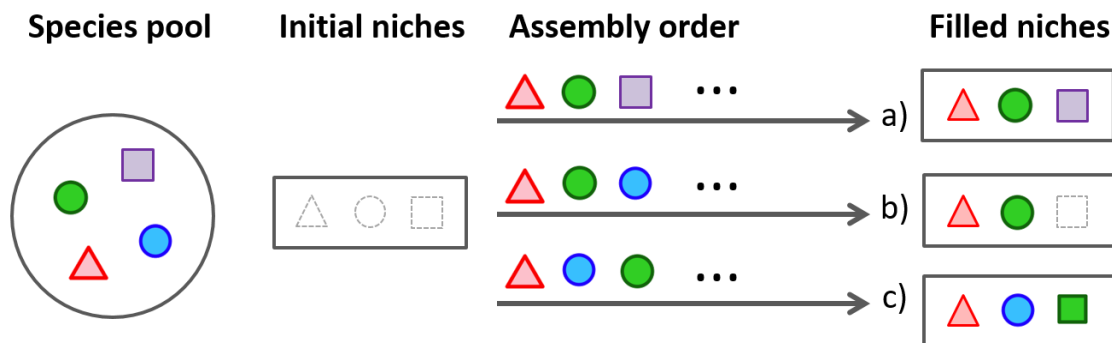
Fig 4. Conceptual representation of mechanisms through which different ecological communities can be formed from the same species pool: i) All species occupy independent niches; ii) An incumbent species blocks an ecologically similar species from joining the community through priority effects by niche pre-emption; iii) Priority effects blocks access to an ecologically-similar species, but niche shifts (i.e. ecological character displacement) facilitates species coexistence and community assembly as each species occupies independent portions of ecological space. Symbol colours indicate different species. Symbol shapes denote the general ecological niche which that species occupies. Open symbols represent vacant niches.

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[20] We should note that we didn't quantatively assess the thermal ecology of all species, instead our coarse qualitative analysis suggested they were similar in that respect too – the lack of more detailed analysis is simply because I hadn't yet garnered enough research funds to buy the equipment necessary to do so.

Perhaps we can draw clues to the differences between species in their degree of ecological lability from their evolutionary history. Those species originating from more diverse communities may have experienced a greater diversity of biotic interactions throughout their recent evolutionary history, and therefore be pre-adapted to mediate biotic interaction to facilitate coexistence[21]. In this example, as *A. extremus* has been isolated on Barbados for ~6my it would, therefore, be presumably less labile than *A. leachii* (which occurs on Antigua and Barbuda with *A. wattsi*), and far less than *A. grahami* (which is from the more speciose Jamaican community; Fig 5)[22]. This unequal degree of ecological lability (think of it as the extent to which a species can be ecologically 'flexible') between species may explain broad patterns in ecological community assembly dynamics and community diversity, and could be an interesting hypothesis to explain non-random macroevolutionary patterns, such as phylogenetic tree imbalance and a clustered community phylogenetic structure.
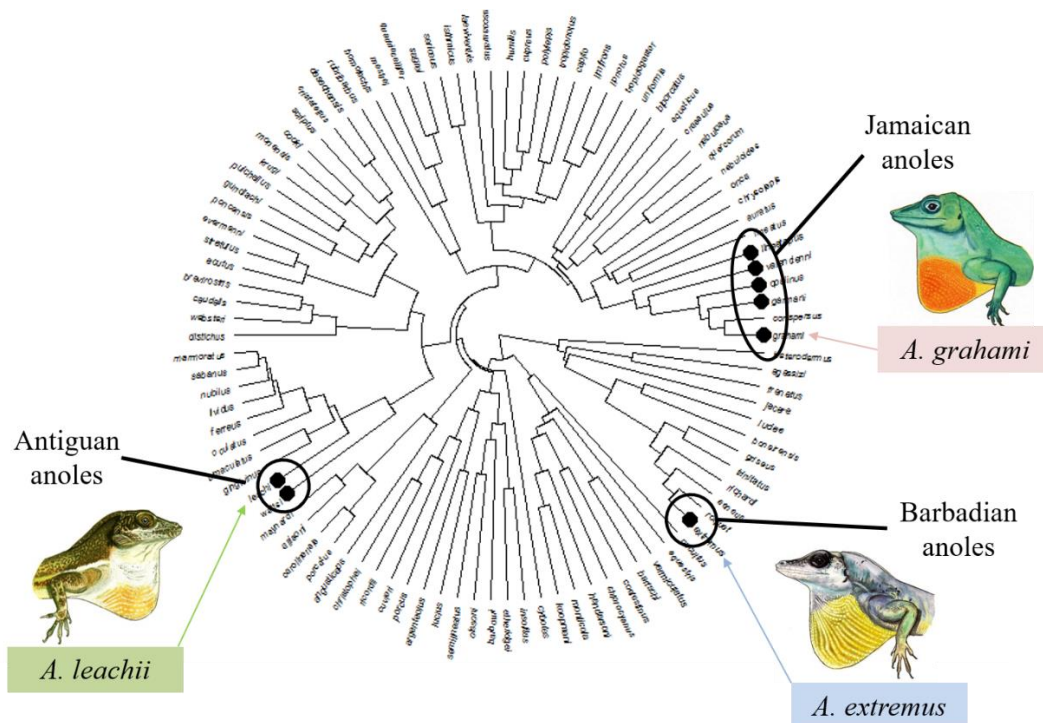
Fig 5. The phylogenetic distribution of each introduced anole in Bermuda, grouped alongside the species with which they co-occur in their native distributions. Anole illustrations are used with permission from Schwartz & Henderson (1985).

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[21] Although the acute readers among you (if anyone has made it this far) will notice this opposes what I had earlier suggested when discussing ecological release.

[22] I should note that this idea has not been well-received at all during the peer review process (as one might expect when throwing an idea out there with little [some journal Editor's may have argued "*no*"…] support). Consequently, as this may otherwise never see the light of day, I think it's a curious hypothesis to float to this forum.

Aside from the unsupported perspectives, this research highlighted two things that deserves further attention in anoles. First, we still don't really understand the role of priority effects in anoles (either ecological or evolutionary). Twenty-five years ago, Losos et al. (1993) investigated how priority effects may influence the outcome of anole invasions. Although this study didn't explicitly refer to priority effects *per se*, it was an investigation into the how niche incumbency might influence the success of contemporary anole invasions. Since then there have been many more anole invasions into a much greater diversity of incumbent communities. This study deserves revisiting[23], and presents an exciting opportunity for further investigation in a burgeoning research area (see Fukami 2015). Secondly, a more comprehensive understanding of character displacement is needed, but especially in how character displacement may operate at range edges or as an ongoing process (perhaps facilitator) during range expansion and invasions. As noted by Losos (2009), and supported (with unashamed bias) by me, south Florida offers great possibilities for doing so[24]. I will now briefly discuss a detailed case study of character displacement from there.

(2.b *Character displacement*)

If we think back to the early stages of adaptive radiation immediately following speciation, those nascent species are expected to be reproductively isolated but may not have diverged in any other aspect of their phenotype (as would be expected if, for example, the two species were allopatric but occupied similar habitats). Upon secondary contact, those species would interact strongly due to the phenotypic similarity, leading to either competitive exclusion or divergence (i.e. character displacement). Through repeated bouts of this process, an adaptive radiation of extraordinary ecomorphological disparity might form. Unfortunately, opportunities to study novel contact zones of phenotypically-similar but reproductively isolated species are rare in the natural world of anoles. The most wonderful experiment to test these hypotheses would be to throw together two species of the same ecomorph and see what happens. However, for all sorts of ethical reasons, this approach is often unreasonable and unattainable.

However, introduced species offer scenarios analogous to these experiments, and I stumbled upon one in Miami (Fig 6). In the late 1970's, the Puerto Rican crested anole (*A. cristatellus*) was introduced to the Pinecrest region in south Miami, which was already home to

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[23] For example, it was suggested that the failure of some trunk-crown-type anoles (*A. ferreus* and *A. extremus*) to establish in Miami was due to priority effects imposed by *A. carolinensis*. Since then, two new trunk-crowns have invaded and become established (*A. chlorocyanus* and *A. allisoni*), suggesting this hypothesis may not be well supported.

[24] The presence of 3 trunk-ground species (*A. sagrei, A. cristatellus, A. cybotes*), 3 trunk-crown species (*A. carolinensis, A. chlorocyanus, A. allisoni*…4 if you include *A. porcatus*), and 2 crown-giants (*A. equestris* and *A. garmani*) provide ample and exciting opportunities for doing so.

several established non-native anoles. However, the introduction of *A. cristatellus* was different. For the first time, a second species of one ecomorph class was entering the community – the Cuban brown anole (*A. sagrei*) had already been present there for many decades. Each of these species, having never coexisted previously and deeply separated in evolutionary time, were members of the trunk-ground ecomorph class. Again, I wasn't particularly original in choosing to study the interaction between these two species – Salzburg (1984) had provided a nice study of the coexistence patterns during its formative years, and Losin (2012) had followed this up with some fabulously detailed behavioural studies. This system was not just unique in that both species occurred sympatrically, but that there also exists allopatric sites within Miami; this presented a wonderful framework with which to conduct a comparative study of character displacement.

🔴 *A. sagrei*
Cuba

🟡 *A. cristatellus*
Puerto Rico
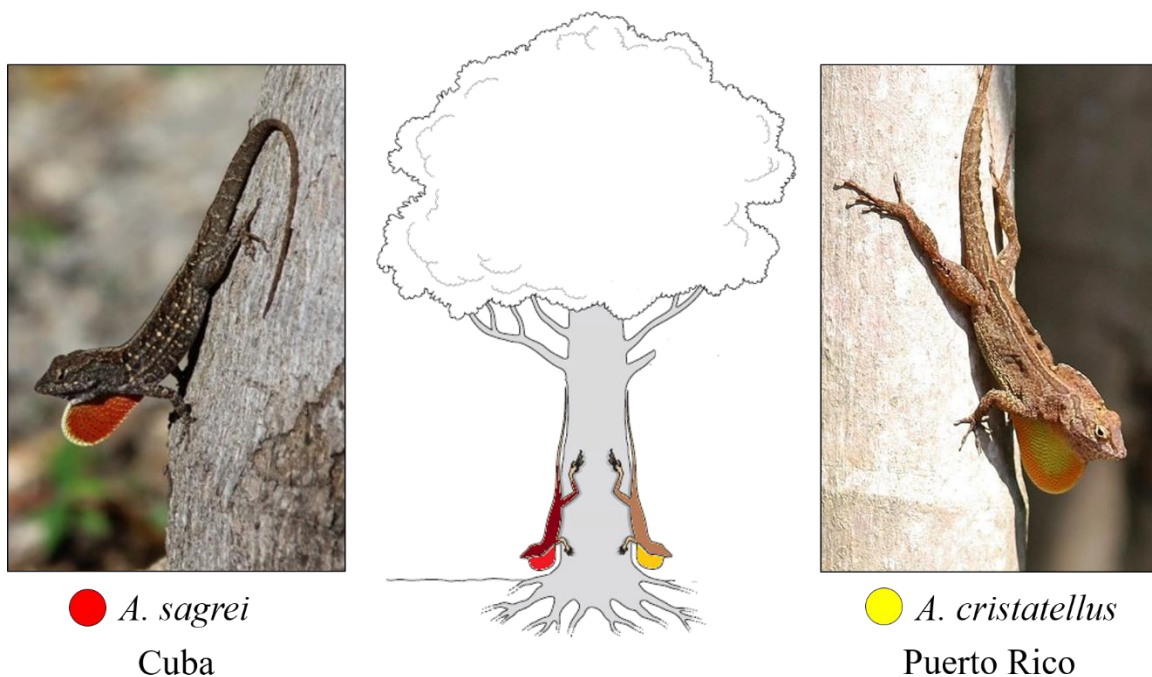
Fig 6. Two introduced Trunk-Ground anoles established in Miami, FL; the Cuban brown anole (*A. sagrei*; left) and the Puerto Rican crested anole (*A. cristatellus*; right).

The presence of ecological character displacement in sympatric communities of *A. sagrei* and *A. cristatellus* in Miami is clear and consistent from very simple data collection on perch use; *A. cristatellus* perches higher (increases in arboreality) and *A. sagrei* perches lower (increases in terrestriality), whereas in allopatry they occupy similar perch heights. Perch height is a common axis along which species partition the environment in anole communities, and it has been repeatedly seen to also occur when previously-allopatric species come into contact[25].

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[25] Yoel Stuart's work on the effect of *A. sagrei* invasion on the ecology of native *A. carolinensis* in Florida is probably the most famous recent example of this (Stuart et al. 2014), but there are also many others.

However, whether this divergence in perch height had shifted the selection regimes that each species encountered, such that it has led to morphological shifts, remained to be seen.

My comparative assessments of morphology showed that both species also had consistent differences between allopatric and sympatric populations. An increase in terrestriality of *Anolis sagrei* led to morphological changes as expected by the form-function relationship in anoles; sympatric populations had fewer toepad lamellae (suggesting relaxed selection on clinging force) and longer limbs (suggesting directional selection for faster sprint speed on broad surfaces, such as the ground). However, I observed no complementary differences in *A. cristatellus* as predicted under this relationship; an observed increase in arboreality did not lead to larger toepads or toepads with more lamellae (as one might expect if an increase in arboreality lead to directional selection for greater clinging force). Instead, the only aspect of the morphology of *A. cristatellus* that showed any significant differences was head size; populations sympatric with *A. sagrei* had significantly smaller heads than those without. Intuitively, head morphology can often be driven by diet. And so, we conducted an extensive and exhaustive assessment of stomach contents of *A. cristatellus* from allopatric and sympatric communities. These investigations revealed no difference in the type or size of prey, the two axes of diet which might lead to differences in head size (for example, larger or harder prey items might need larger heads to managed them). In all cases in Miami, both *A. sagrei* and *A. cristatellus* are generalist invertivores and show little variation among populations[26].

Head shape and size is not only an important predictor of trophic ecology, but many studies (in anoles as well as other lizards) highlight its importance in the light of sexual selection. Larger heads generally bite harder[27] and biting hard can be an important determinant of the outcome of agonistic interactions. Presumably there are fitness consequences associated with winning or losing those interactions. Perhaps a change in the (intraspecific) social landscape of *A. cristatellus* when sympatric with *A. sagrei*[28] has led to a shifting regime of sexual selection, which may explain differences in head size.

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[26] Although we did observe that the source of prey in *A. sagrei* changes slightly; *A. sagrei* eat more ground-dwelling arthropods when sympatric with *A. cristatellus* (presumably as a result of it being on the ground more…).

[27] We conducted performance assessments of bite force of *A. cristatellus* in Miami which support that this is true for this case study specifically.

[28] I can't claim originality for this idea either – Sandy Echternacht presented a beautiful perspective in the *Anolis* Newsletter V (p.23) proposing how the availability of territories for *A. carolinensis* might change due to the presence of *A. sagrei*. This small figure had a profound impact on how I thought about interspecific interactions (and the consequences of ecological divergence).

Fig 7. The progression of an aggressive male-male social interaction between Puerto Rican crested anoles (*A. cristatellus*). Increased head size, which corresponds with increased bite force – an important predictor of success in aggressive combat, might be favored in populations with high levels of intraspecific social interactions.

Fig 8. Bite marks from a conspecific male are apparent on the shoulder/dorsum and forelimbs of this male crested anole (*A. cristatellus*). The agonistic interaction which led to these marks was observed (so their source are known), with the lizard easily noosed as it lay stunned on the ground having been usurped.

To investigate this hypothesis I approached it from two angles; ethological observations of natural behavior (which I am eternally indebted to Sarin 'Putter' Tiatragula for spending long, buggy days helping out with) and analysis of the social networks of marked individuals (an approach I developed with Rob Heathcote). In short, data collected from these two approaches highlighted that when *A. cristatellus* are sympatric with *A. sagrei* they; (i) move between trees in their environment significantly less, (ii) have relatively fewer conspecific interactions with other *A. cristatellus*, and (iii) low conspecific interactions was driven by high interspecific interactions with *A. sagrei*.

Instead, as an indirect effect of increased arboreality, concomitant with decreases in population size and relative abundance, *A. cristatellus* become (intraspecifically) socially-isolated. This has relaxed selection on sexually-important traits associated with intraspecific interactions, specifically bite force, and led to a decrease in head size in sympatry. I suggested that simple ecological character displacement, such as vertical partitioning of habitat as observed here, can lead to phenotypic divergence much more complex than anticipated, and therefore may be responsible for a greater volume of observed phenotypic variation than previously recognized.

A classic model of character displacement might expect ecological divergence to occur along one resource axis, with concomitant divergence in traits associated with the acquisition of that resource. For example, a divergence in seed size in finches might lead one to expect selection for large bills in the species that shifts to large seeds and small bills in the species that eats small seeds. In anole terms, divergence in perch diameter might lead one to expect selection for longer limbs in the species that shifts to broader perches and smaller limbs in the species that shifts to thinner perches; this is a classic [symmetrical] model of character displacement.

Here, I suggest that apparently simple ecological divergence along one resource axis (perch height) can profoundly impact the new selection regimes facing each species. Following this more complex model, resource partitioning in structural habitat (such as perch use) may drive phenotypic diversification far quicker than previously appreciated.

Conservation implications of introduced species

It is important to be aware that non-native species, whilst occasionally providing exciting – if unintended – opportunities for eco-evolutionary studies, can also negatively interact with native species and pose a conservation threat. It would be irresponsible of any ecologist or evolutionary biologist using introduced species as a model system to not acknowledge this. As a result of my research investigating the range dynamics and assembly patterns of anoles on Bermuda, Sean Giery and I also discovered two independent populations of brown anoles (*A. sagrei*; Stroud et al. 2017)[29]. Bermuda has only one endemic lizard, the Critically Endangered Bermuda skink (*Plestiodon* [*Eumeces*] *longirostris*) (Wingate 1965, Davenport et al. 2001; Fig. 9), which are terrestrial, leaf-litter specialists, and are similar in size and other aspects of their ecology to *A. sagrei*. At present, the populations of *A. sagrei* that we identified are still locally distributed and confined to urban areas where Bermuda skinks are

Fig 9. The Critically Endangered Bermuda skink (*Plestiodon longirostris*), endemic to the Bermuda archipelago and one of the rarest lizards in the world with a total global population of ca. 3,500 individuals. Photographed on Nonsuch Island, Bermuda. Not an anole, but a nice lizard nonetheless.

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[29] I used "discovered" very loosely here – we provided the first official record. Joe Macedonia must take credit for this discovery having posted pictures of Bermudian *A. sagrei* on *Anole Annals*, which led us to seek them out.

not present[30].

We were awarded a small grant from the Bermuda Zoological Society to assess the potential ecological impact that *A. sagrei* might have on Bermuda skinks were they to invade known populations. We conducted detailed assessments of habitat use, diet, population size, and morphology, and concluded (due to high overlap with skinks in all) that *A. sagrei* likely pose a significant conservation threat to Bermuda skinks via ecological resource competition. These findings strongly highlight that continuing to monitor the distribution and ecology of *A. sagrei* on Bermuda should be considered an important aspect of Bermuda skink conservation management. As anoles continue to spread far and wide around the world, I expect this situation to continue to become increasingly more common; this study might provide a framework which others can adopt.

Conclusions

If you have got this far, thank you for sticking with it – those discussions presented an overview of my dissertation research, as well as various topics of current or future research interests (alongside some general commentary on anole ecology and evolution). Broadly, I add to the body of evidence in anole research that character displacement can both facilitate coexistence and drive phenotypic change, therefore strengthening the importance of the process in explaining patterns of ecology and evolution.

I conclude with two points from my introduction to anole biology over the past few years: (i) the utility of anoles as a model system for testing broader hypotheses in ecology and evolution is more powerful now than ever before, in no small part due to the foundational work that so many of you have dedicated your research careers towards, and (ii) there is still an awful lot that we don't know about anoles!

If any of the topics I have highlighted here interest you then please feel free to reach out and get in contact. I would be excited to discuss some of these ideas further, and I am always looking for new research collaborations!

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[30] Incidentally we also described the first *verified record of an American green anole (*A. carolinensis*) on Bermuda, although we presume this was only a single specimen (Stroud et al. 2016). *Verified because there is a record of *A. carolinensis* on Bermuda from an expedition to Bermuda by the American Zoologist G. Brown Goode in 1867 (then erroneously labeled "*A. principalis*"), but no specimen is available for analysis. Either way, there is no evidence that a population did (or now does) exist on Bermuda.
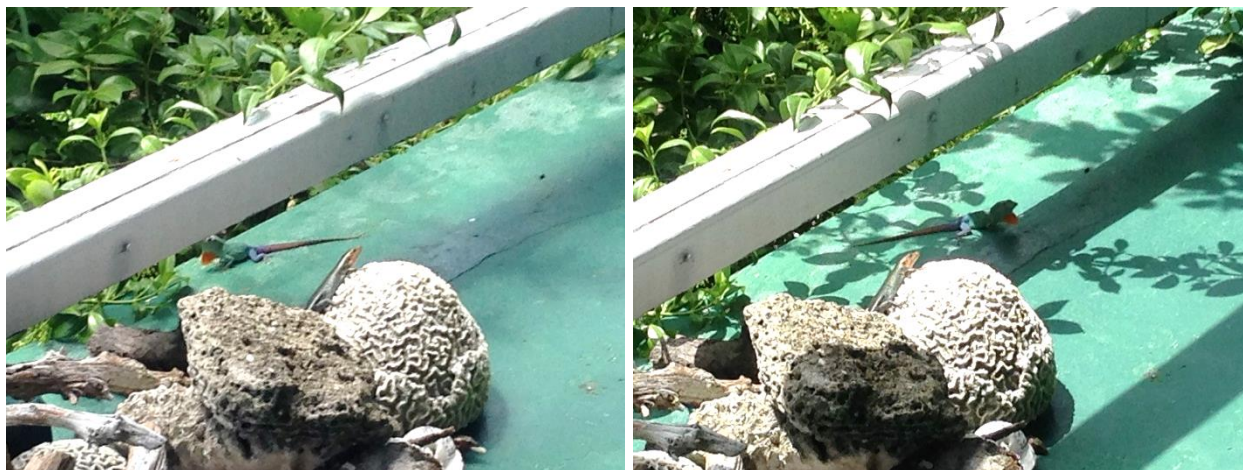
Fig 10. A Jamaican anole (*A. grahami*) displaying at a Bermuda skink (*P. longirostris*) on Nonsuch Island; one of the last large populations of Bermuda skinks in the world. This, of course, has nothing to do with what I have just written, but I thought it's a unique opportunity to point out some distant relatives communicating.

Future directions

In 2018, I started a postdoctoral position in the Losos Lab. The majority of my time will be spent understanding how patterns of natural selection in anole communities facilitates coexistence. This stems from a project in Miami that I have been conducting for multiple years on the introduced species there (although one that I didn't discuss in this contribution). I will attempt to extend this project to include natural communities across the replicated adaptive radiations of the Greater Antilles (specifically; Jamaica, Dominican Republic, and the Bahamas). This project aims to understand the nature of natural selection in anole communities through space and time and will hopefully give some insights into the structure and topography of fitness landscapes in anole communities.

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