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Evolution of a Model System: New Insights from the Study of *Anolis* Lizards

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Abstract

With decades of intensive study, *Anolis* lizards have emerged as a biological model system. We review how new research on anoles has advanced our understanding of ecology and evolution, challenging long-standing paradigms and opening new areas of inquiry. Recent anole research reveals how changes in behavior can restructure ecological communities and can both stimulate and stymie evolution, sometimes simultaneously. Likewise, investigation of anoles as spatial or phylogenetic evolutionary experiments has documented evolutionary repeatability across spatiotemporal scales, while also illuminating its limits. Current research places anoles as an emerging model for Anthropocene biology, with recent work illustrating how species respond as humans reconfigure natural habitats, alter the climate, and create novel environments and communities through urbanization and species introduction. Combined with ongoing methodological developments in genomics, phylogenetics, and ecology, the growing foundational knowledge of *Anolis* positions them as a powerful model system in ecology and evolution for years to come.

1. INTRODUCTION

1.1. Anoles as a Model System in Ecology and Evolution

Model systems—species or sets of species studied in great depth by a research community—play a special role in the biological sciences. When a particular study system is simultaneously approached from multiple disciplinary angles over many years, the cumulative knowledge generated propels scientific inquiry into new frontiers. Such systems yield insights that would be elusive without a robust foundation of prior knowledge and can, in turn, prompt novel questions and avenues of inquiry to be investigated across the tree of life. Indeed, a hallmark of a productive model system is that continued study, rather than yielding diminishing returns, produces new discoveries, insights, and perspectives.

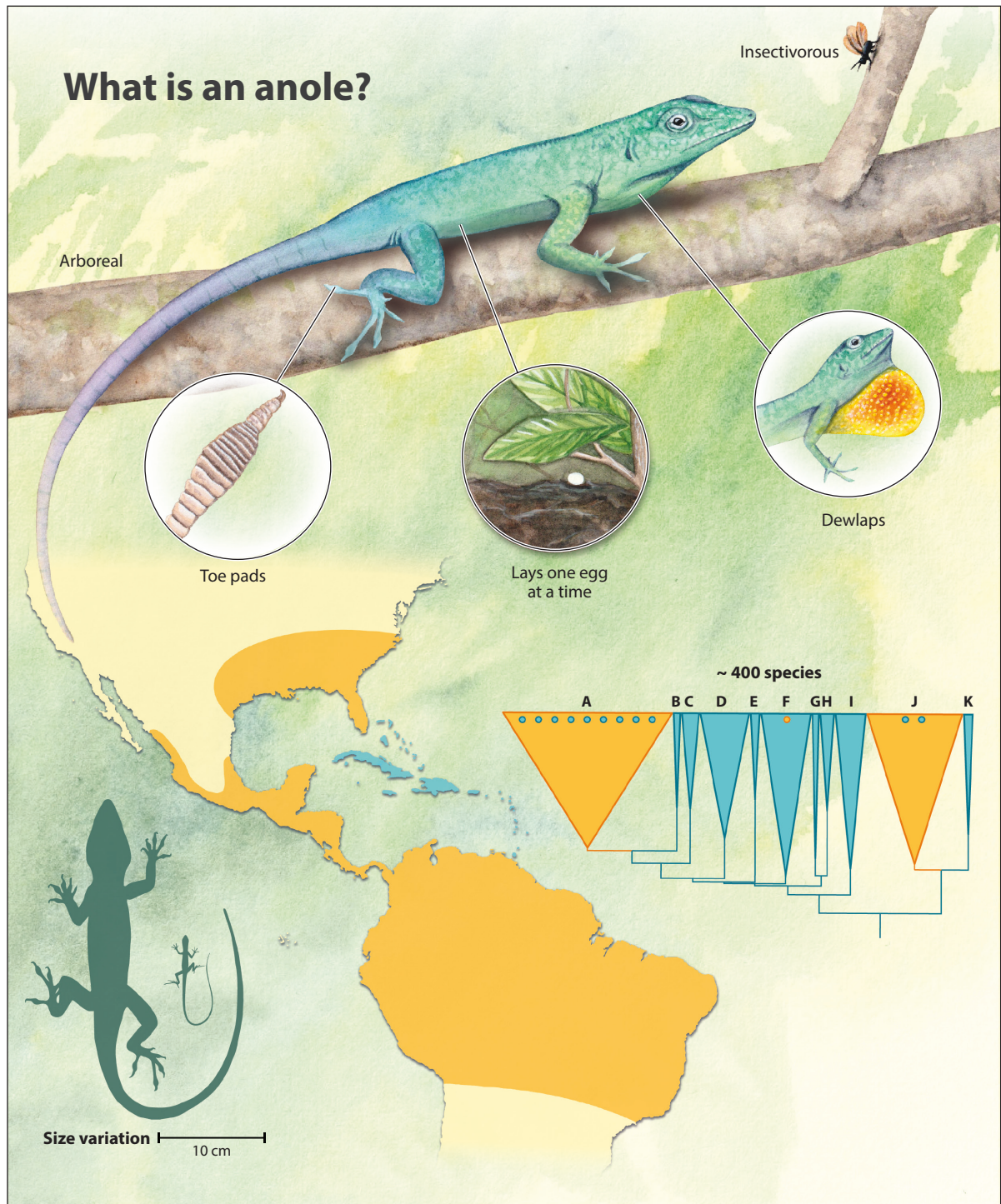
Over many decades, the Neotropical lizard genus *Anolis* emerged as a powerful model system in ecology and evolution (Williams 1969, 1983; Losos 1994, 2009). Since the 1960s, empirical research on anoles has shaped our fundamental understanding of ecological and evolutionary topics, from mechanisms of community assembly to the process of adaptive radiation (Losos 2009). The emergence of anoles as a model system was not coincidental. Anoles are an appealing model because they are often abundant, they have relatively short generation times, and they exhibit variation in numerous attributes of interest to ecologists and evolutionary biologists that is independently replicated across space and at multiple scales of organization (e.g., from local communities to regional faunas and from populations to entire clades).

In this review, we examine how recent research on *Anolis* lizards has generated novel insights into ecological and evolutionary biology, in many cases reframing long-standing paradigms. We first review the features of *Anolis* that make them especially compelling study subjects (Section 1). We then examine how recent research on anoles has refined our collective understanding of major concepts in ecology, evolution, and Anthropocene biology. We highlight that deeper exploration of species interactions and behavior reframes our understanding of ecology, community dynamics, and evolution (Section 2). We then show how short-term anole evolution experiments and advances in anole phylogenetics have helped answer long-standing questions about the rate, pattern, timing, and spatial dynamics of evolution at multiple scales (Section 3). Lastly, through cross-cutting research focused on rapid environmental change, anoles are illustrating the strategies by which species tolerate an increasingly anthropogenic world (Section 4). By building on decades of foundational knowledge, the modern wave of anole research provides an integrative, hierarchical understanding of ecology and evolution and paves the way for further advances.

1.2. What Is an Anole?

Anoles are a diverse clade of iguanian lizards distributed throughout the Neotropics. They are small to medium sized (usually 1–100 g), diurnal, typically arboreal, and primarily insectivorous (Losos 2009) (**Figure 1**). The bodies of most species are green, gray, or brown, but anoles exhibit great color diversity in characteristic throat fans, called dewlaps. Males of nearly all species possess dewlaps, as do females of some species, although female dewlaps are typically smaller. Anoles dynamically expand and retract their dewlaps, often in combination with headbobbing movements and push-ups, to create species-specific displays for courtship, territory defense, and other social communication (**Figures 1, 2**). Anoles' arboreality is achieved through adhesive toe pads composed of expanded scales (lamellae), which are carpeted by fine filaments, or setae, that stick to surfaces through electrostatic forces (**Figure 1**).

With over 400 species (and counting), anoles are conspicuously diverse (Losos 2009). The Caribbean islands are home to >150 species, and >250 others are found in southern North America, Central America, and northern South America. Anoles are ubiquitous throughout the



(Caption appears on following page)

Figure 1 (Figure appears on preceding page)

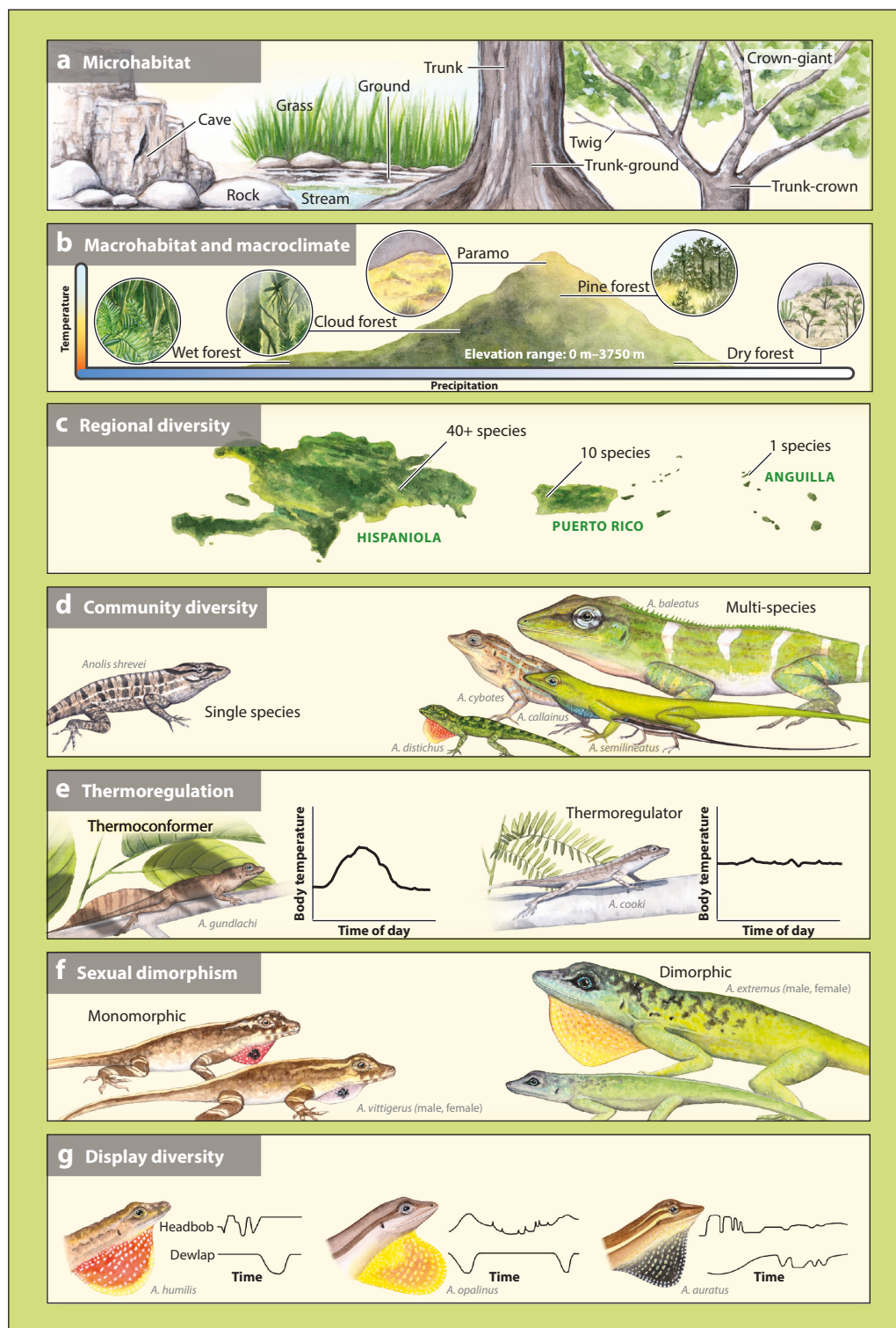
Anoles are a diverse radiation of Neotropical lizards. They are small to medium sized (for the range of adult body sizes observed among species, see the inset), are primarily insectivorous, and lay a single egg at a time. They can extend a retractable throat fan (the dewlap) for communication and possess adhesive toe pads that provide clinging capacity (illustrated here by the Jamaican trunk-crown specialist *Anolis grahami*). Anoles are distributed in both continental (*orange*) and island (*blue*) regions. Major subclades within *Anolis* are illustrated as triangles in a simplified phylogeny. Triangle depth indicates relative subclade age, triangle width reflects relative species diversity, and letters indicate subclade names as follows: A, Draconura; B, Placopsis; C, Trachypilus; D, Ctenonotus; E, Audantia; F, Ctenocercus; G, Schmidtanolis; H, Xiphosurus; I, Deiroptyx; J, Continenteloa; and K, roquet series. Clades are colored according to the type of region (continental or island) occupied by most species, and colored dots indicate the inferred number of independent colonizations of the other region type by members of a given clade (each reflecting only a single species). Phylogeny reproduced from the time tree of Poe et al. (2017). Illustrations provided by Julie Johnson of Life Science Studios.

Caribbean, found on all but the tiniest of West Indian islands (Williams 1969), and in two instances have colonized remote Pacific islands (*Anolis agassizi* on Malpelo Island and *Anolis townsendi* on Cocos Island). Only one species (*Anolis carolinensis*) is native to the southeastern United States, but several Caribbean species have invaded the region, and some have likewise been introduced to other tropical or semitropical locations across the globe (Helmus et al. 2014). Anoles have achieved their present natural distribution through a sequence of infrequent interregion colonization events followed in several early cases by prolific regional diversification (Poe et al. 2017, Patton et al. 2021, Landis et al. 2022). Phylogenetically, this process has resulted in two independent continental radiations and two archipelagic radiations, as well as nearly a dozen island-dwelling endemic species with relatively recent mainland ancestry (**Figure 1**).

1.3. Multiple, but Not Limitless, Dimensions of Replicated Diversity in *Anolis*

Anoles emerged as a compelling model system because of their exceptional diversity across numerous dimensions of abiotic and biotic variation (**Figure 2**). This diversity is geographically and phylogenetically replicated, making the group especially attractive for comparative investigation. Caribbean anoles exemplify adaptive radiation through their diversification into different microhabitats, defined by characteristics of the perches that they most often utilize (e.g., tree trunks, twigs, grasses/bushes, or canopy vegetation). On the islands of the Greater Antilles (Cuba, Hispaniola, Jamaica, and Puerto Rico) six types of specialists (termed ecomorphs) independently evolved shared morphological, ecological, and behavioral features, in turn giving rise to species-rich local communities (Williams 1983, Losos 2009) (**Figure 2d**). Ecomorphological convergence also extends beyond these six types. Cave and karst anoles, for example, have also repeatedly evolved (Losos 2009, Scarpetta et al. 2015), as have stream specialists (Boccia et al. 2021).

Anoles span diverse climates, occurring from the equator into mid-latitudes and from sea level to nearly four kilometers above it. Across these broad gradients, anoles occupy nearly every available habitat, including rain forests, cloud forests, savannas, swamps, pine forests, and deciduous forests (**Figure 2b**). While absent from true deserts, anoles inhabit xeric scrub and coastal dunes. In response to such varied environments, anoles are physiologically diverse (Salazar et al. 2019, Muñoz 2022). High-elevation and high-latitude anoles, for example, are more cold tolerant than those found in warmer environments (Gunderson et al. 2018, Salazar et al. 2019). Within regions, species that utilize sunny open habitats are more heat tolerant than relatives found in cool, shaded environments (Gunderson et al. 2018). Accompanying this physiological variation are diverse behavioral strategies: Whereas some species allow their body temperature to passively fluctuate with the environment (thermoconformers), others actively bask or seek shade to maintain a precise body temperature (thermoregulators) (Logan et al. 2015, Muñoz & Losos 2018, Méndez-Galeano et al. 2020) (**Figure 2e**).



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Figure 2 (Figure appears on preceding page)

Multiple dimensions of diversity in *Anolis*. (a) Anoles are ecomorphologically diverse, occupying a wide range of structural microhabitats and exhibiting a correspondingly broad range of morphological specializations. (b) Likewise, anoles have diversified across elevation and latitude in numerous macrohabitats and macroclimatic environments. (c) Island species richness ranges from a single species on many small islands to several dozen on Hispaniola (> 40 spp.) and Cuba (> 60 spp.). (d) Such regional richness is partitioned into community-level richness, which varies from a single species to roughly a dozen species. (e) Anoles vary in thermoregulatory strategy. Some populations and species are behaviorally passive thermoconformers, and others are precise thermoregulators. (f) Whereas some species are monomorphic, others are highly sexually dimorphic, particularly in body and dewlap size. (g) Anoles exhibit species-specific patterns of headbobs (*upper amplitude trace*) and dewlap extensions (*lower trace*). (a–d) From left to right, according to the position of the eye, the species illustrated are (d) *Anolis shrevei*, *A. distichus*, *A. cybotes*, *A. callainus* (until recently *A. chlorocyanus*), *A. baleatus*, and *A. semilineatus*; (e) *A. gundlachi* and *A. cooki*; (f) *A. vittigerus*, male and female, and *A. extremus*, female and male; and (g) *A. humilis*, *A. opalinus*, and *A. auratus*. Illustrations provided by Julie Johnson of Life Science Studios.

Anoles exhibit a range of regional diversity patterns (**Figure 2c**). Islands of the Lesser Antilles are home to only one or two native anole species, and islands in the Great Bahamas Bank host up to four. The Greater Antilles support richer faunas, ranging from 6 species (Jamaica) to over 60 (Cuba), primarily reflecting prolific in situ (i.e., within-island) speciation (Losos & Schluter 2000). Variation both in species richness and in the mechanisms by which such richness accumulates offers a rich framework for studies of biogeography and diversification (Losos & Schluter 2000; Mahler et al. 2010, 2013; Algar & Losos 2011). Anole species richness also varies at local scales. Local community richness can reach roughly a dozen species (Anderson & Poe 2019) and varies along numerous ecological and anthropogenic axes (Frishkoff et al. 2019). For example, only a single species, *Anolis shrevei*, occurs above the tree line in the central mountains of Hispaniola; by contrast, a single patch of moist forest in the lowlands is often occupied by five species (**Figure 2d**). Communities with the same number of species need not contain the same functional diversity (Anderson & Poe 2019). Whereas some communities on the mainland contain multiple morphologically similar species, communities in the Caribbean often have single representatives of each of the morphologically distinct ecomorphs. The degree of species turnover across space (i.e., beta diversity) varies within and among mainland and island habitats (Algar & Losos 2011, Stuart et al. 2012, Frishkoff et al. 2022). For example, spatial turnover is low on Jamaica, where most species exist essentially island wide. Hispaniola, by contrast, has several regional faunas, with complete species replacement across space and across hydric and thermal environmental gradients. Such variation in community richness, functional composition, and species turnover provides a compelling substrate for studies in community ecology.

Despite their diversity, some anole features are surprisingly invariant. Although squamate reptiles (lizards and snakes) are famously labile in reproductive mode and clutch/litter size, anoles are exclusively oviparous and lay single-egg clutches (**Figure 1**). No anoles are nocturnal, and the group never evolved dietary specializations observed in other vertebrate clades, like exclusive herbivory. These features preclude some questions from being explored with anoles but simultaneously augment the analytical tractability of the group for other topics (e.g., diurnality means anoles compete only for diurnally available prey).

2. BEHAVIORAL AND COMMUNITY ECOLOGY

2.1. What Structures Anole Communities? Traditional Views and Newer Models

Anoles emerged in the mid-twentieth century as a study system amenable to community ecology. Over the following decades, anole research contributed to our broader understanding of community assembly processes, with landmark work illuminating the importance of competition and niche partitioning for coexistence (e.g., Roughgarden 1974, Schoener 1975, Lister 1976, Rummel & Roughgarden 1985). Many classic ideas are receiving renewed attention today with new insights

from behavioral ecology, biogeography, and niche modeling, as well as a broader consideration of community types, particularly on the mainland, where anoles are less numerically dominant than in the Caribbean. Still, different studies often point to divergent answers to the question of what structures communities. In the following subsections, we highlight the ways that predation, food limitation, competition, and geographic area contribute to patterns of community richness. Anoles are a model for ecology and evolutionary biology in part because they form numerous largely evolutionarily independent faunas across the Neotropics, facilitating comparative inquiry. Going forward, parallelizing observational and experimental studies across geographic regions (e.g., mainland versus islands, multiple islands with different characteristics) will help address the roles of alternative drivers in setting levels of diversity and phenotypic variation across anole communities.

2.1.1. Top-down versus bottom-up control. Community ecologists have long debated the relative importance of predation (top-down control) and food limitation (bottom-up control) in structuring communities. Testing the impact of predation on community interactions is challenging due to difficulties in conducting the relevant experiments (Calsbeek & Cox 2010, Losos & Pringle 2011). Creative new studies, however, have begun to tackle this topic and hint that predation's role in structuring prey communities may be as much psychological as consumptive. When predators are experimentally introduced to anole communities, the number of documented instances in which predators consume anoles as their prey is surprisingly small (Pringle et al. 2019). Instead, anoles are wary and tend to avoid areas where potential predators forage. This restricts their own ability to consume insect prey, ultimately leading to lower *Anolis* abundance. This behavioral avoidance of predators operates similarly to interference competition between anole species (Culbertson & Herrmann 2019). If such fear-driven avoidance behavior is widespread (Laundré et al. 2010), then this mechanism may partly explain observed differences in structure between mainland and island anole communities. Islands tend to have fewer predators and denser populations of behaviorally conspicuous anoles than mainland habitats, and island anole communities tend to be partitioned among larger numbers of distinct ecomorphs, presumably due to greater competition with other abundant anole species (Andrews 1979, Poe & Anderson 2019, Patton et al. 2021).

Substantial classic evidence suggests that anoles are frequently prey limited (e.g., Licht 1974). Recent evidence continues to support this view: Seaweed additions that increase invertebrate densities on small Caribbean islands can increase anole growth rates and reproductive output (Wright et al. 2013), ultimately fostering higher population sizes (Wright et al. 2020). The situation is less clear on the mainland. Drawing upon numerous lines of indirect evidence, Andrews (1979) suggested that predation, rather than food limitation and competition, should control anoles on the mainland. However, classical evidence for this idea is equivocal, and the single direct experimental test of food limitation on the mainland found evidence for it (Guyer 1988)—though it should be noted that the species studied, *Anolis humilis*, is an unusually abundant mainland anole. Food limitation experiments have yet to be repeated elsewhere on the mainland and represent an untapped opportunity to resolve the relative roles of top-down versus bottom-up control across tropical communities.

2.1.2. Competition. Given that anole communities frequently appear to be food limited, competition between species (especially exploitative competition, i.e., drawing down the same resource, thereby limiting population sizes) could strongly shape community structure. Whether exploitative competition exists depends on whether species use the same resources, necessitating the study of *Anolis* dietary niche overlap. Direct studies of anole diets have typically assessed the size and taxonomic order of stomach contents. Both classic and modern studies have uncovered a diversity of results, with many species substantially overlapping in diet [high overlap recorded on



Jamaica (Lister 1976) and recently on Puerto Rico (Ingram et al. 2022)], though cases of strong dietary divergence between species also exist (Schoener 1968). However, whether competition exists or not depends on the demographics of prey populations, and it is possible for single insect orders (or size classes) to contain multiple ecologically distinct resource pools (e.g., different beetle species may localize to different microhabitats, allowing canopy-dwelling and ground-dwelling lizards to avoid competing despite having extensive dietary overlap at the level of taxonomic order). As such, without quantifying diet to finer taxonomic resolution, observational studies are ill equipped to rule out dietary differentiation, especially in cases where the prey consumed is very similar at the order level.

Finer resolution is now afforded by DNA barcoding, an approach used by Pringle et al. (2019) to resolve diet content from anole feces collected from small experimental islands in the Bahamas. In contrast to some past studies based on visual identification of stomach contents, Pringle et al. (2019) found that *Anolis sagrei* (a trunk-ground species), differed substantially in diet from co-occurring *Anolis smaragdinus* (a trunk-crown species), suggesting that dietary niche partitioning is, in fact, quite strong. This dietary difference was eliminated following a predator-induced increase in microhabitat overlap between these species, suggesting that by providing alternative insect resource pools, microhabitat specialization was the primary mechanism of dietary differentiation. Likewise, stable isotopes offer a complementary means of assessing dietary overlap. In seminatural outdoor experimental enclosures on Hawai'i, green anoles and brown anoles (both nonnative) demonstrated substantial differentiation in dietary niche. Furthermore, isotopic dietary signatures were unaltered when species were alone versus in combination, suggesting that prospective competitor presence by itself did not induce major dietary shifts (Figueira et al. 2023). To date, these technologies have been applied only in single systems, precluding generalization. In the future, wider adoption of DNA-based methods (Kartzin et al. 2015) and isotopic approaches (Figueira et al. 2023) will hopefully illuminate the degree to which anole dietary niches overlap.

Recent work has added evidence that the outcome of competition scales up from individual interactions to shape local communities. Past experimental manipulations on small Caribbean islands and Puerto Rico illustrated that the presence of other anole species can limit establishment success, restrict growth rates, or depress population sizes (reviewed in Losos 2009). Mainland species appear to also limit one another competitively: When mainland *Anolis apletophthalmus* was introduced to small islands within the Panama Canal its abundance was lower and extinction rate higher if *Anolis gaigei* (also frequently found in mainland environments) was also present (Nicholson et al. 2022). Whether these competitive effects would also apply to populations in continuous mainland habitat remains uncertain, in part because *A. gaigei* was not experimentally introduced but rather occurred naturally on some islands and not others.

In addition to experiments, researchers have investigated whether competition structures anole communities by testing for its signatures across space. If competition structures communities, then they may become saturated with species, such that even on islands with many species, individual local communities may equilibrate at lower diversities once all niches are filled. This appears to be the case when comparing the islands of Jamaica (6 native species) and Hispaniola (>40 species). Across dozens of 15-m-radius plots in the lowlands of both islands, communities have similar anole abundances and possess roughly five species each. Plots from opposite islands are more similar to one another than expected by chance in both species numbers and average morphologies, providing evidence for convergence at the community level, given the independent evolutionary origin of each island's anole fauna (Frishkoff et al. 2022).

Whereas classical approaches to understanding competition have generally relied on local-scale studies of cooccurrence, behaviors, and diet similarities, the availability of broadscale

species distribution data has also granted new ways to infer the alternative drivers that structure communities. By evaluating climatological variables that predict species occurrence records, and complementing this information with an assessment of morphological similarity with other nearby species, Algar et al. (2013) found evidence that species interactions limit geographic ranges on Hispaniola. Although climate affinities explain many species' range limits on that island, anoles that are similar in morphology are less likely to co-occur than expected based on null models (Algar et al. 2013). This apparent limiting similarity at the range scale was present for approximately one-third of species examined, leaving open the possibility that some species have diverged enough along other ecological axes to no longer be inhibited by competition. Whether general rules govern which anole communities have managed to differentiate themselves sufficiently to eliminate competitive effects awaits more comprehensive evaluation.

2.1.3. Geographic area. Area plays a major role in structuring anole community diversity, and recent research on anoles suggests that a key mechanism behind this relationship arises from the ability of larger regions to foster in situ speciation. Islands less than $\sim 3,000 \text{ km}^2$ are too small for within-island speciation in anoles (Losos & Schluter 2000), resulting in depauperate anole faunas in comparison to larger islands. Recent evidence suggests that similar logic applies to ecologically distinct subregions within islands, and when such regional species pools are severely limited, local community diversity is diminished. The highlands of Jamaica at $< 400 \text{ km}^2$ are environmentally similar to the highlands of Hispaniola at $> 3,000 \text{ km}^2$ but are species poor at the local scale. Only one Jamaican anole evolved to specialize on its highlands. By contrast, Hispaniola possesses species-rich highland communities, composed largely of members of a single clade of highland specialists that diversified in situ early in the Hispaniolan radiation (Frishkoff et al. 2022). Even though the total number of anole individuals is similar between islands as one moves up in elevation, local species richness trajectories diverge above $\sim 500 \text{ m}$, an effect attributable to the diversification of highland specialists on Hispaniola but not Jamaica. If such specialists were eliminated, the species richness trajectories with elevation between Jamaica and Hispaniola would be equivalent (**Figure 3**).

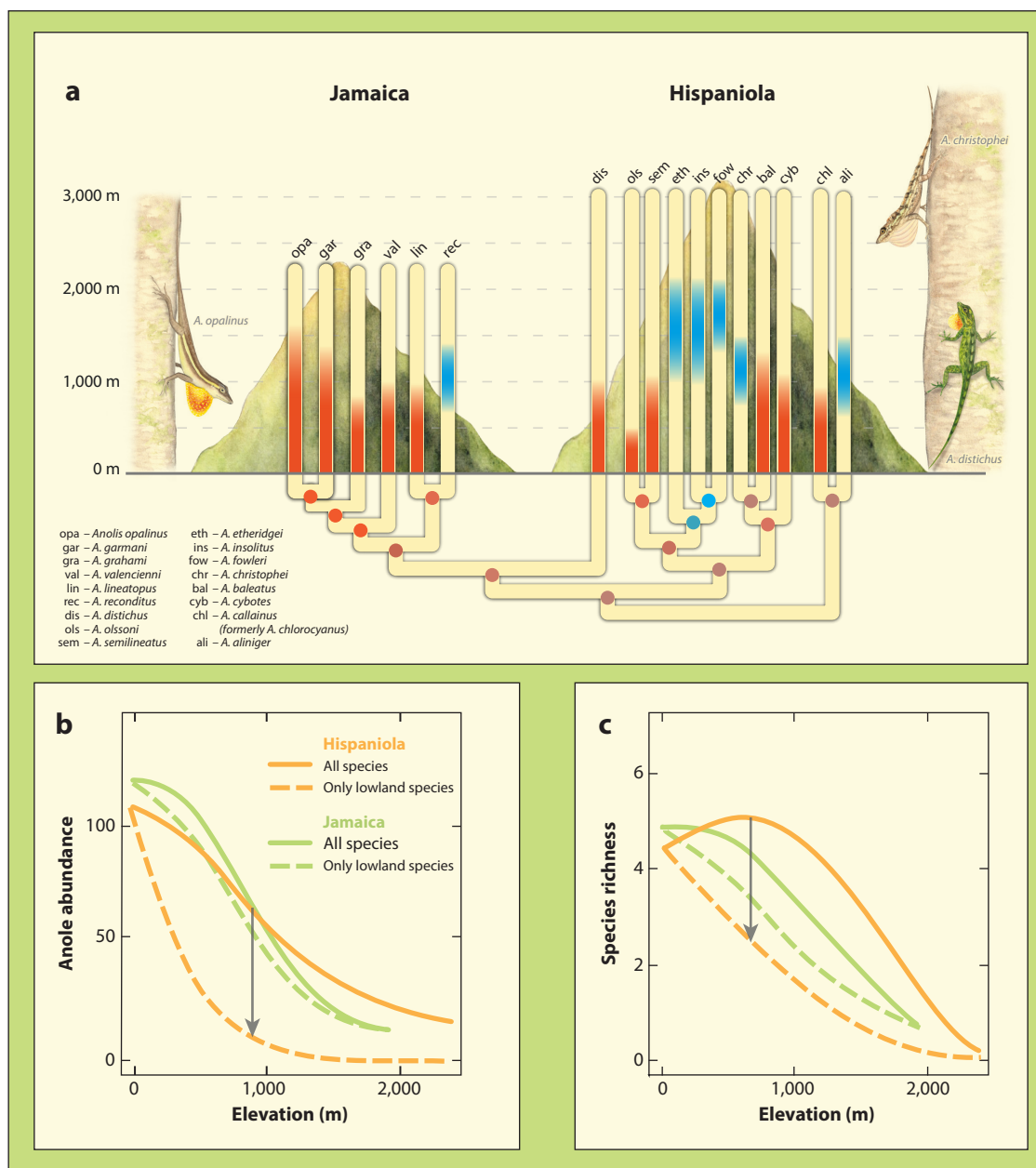
The relationship between area and diversity also differs between the Caribbean islands and the mainland. Based on the theory of island biogeography (MacArthur & Wilson 1967), islands are expected to have fewer species than the mainland. But Caribbean islands large enough to support in situ speciation have more species than similar-sized regions of the mainland, suggesting that predators or nonanole competitors may limit mainland diversity (Algar & Losos 2011). Mainland communities have fewer total morphological types; instead, such communities harbor more species with similar morphologies (Poe & Anderson 2019), supporting the hypothesis that competition is not a strong determinant of mainland communities.

2.2. Behavior as the Linchpin Connecting Anole Ecology, Community Dynamics, and Evolution

To survive, grow, and reproduce, anoles behaviorally interact with their environments. Behavior thus mediates the forces of natural selection that organisms experience. Small and palatable to many larger predators, anoles operate in a landscape of fear (Laundré et al. 2010) that shapes how they interact with their surroundings (Palmer et al. 2022). This landscape influences how anoles display, how they move, and where they perch (Steinberg et al. 2014, Chejanovski et al. 2017), reflecting a trade-off between fitness-enhancing activities and exposure to predators (Losos et al. 2004, 2006; Lapiedra et al. 2018). In the presence of predators, for example, anoles dampen their headbob displays, a behavioral shift that reduces exposure but also decreases their conspicuousness to competitors and mates (Steinberg et al. 2014).



Behavioral responses to predation risk also alter anole community dynamics. As a trunk-ground specialist, the brown anole (*A. sagrei*) typically uses low arboreal perches, from which it jumps to the ground to catch insects. In the presence of the curly-tailed lizard (*Leiocephalus carinatus*), a ground-dwelling predator, *A. sagrei* becomes less terrestrial and moves further up into available vegetation (Losos et al. 2004, 2006) (Figure 4). This behavioral shift is not cost free: Because *A. sagrei* primarily feeds on the ground, its body condition worsens over time in the presence of



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Figure 3 (Figure appears on preceding page)

(a) Differences in local community richness between islands are attributed to differences in highland area, which foster the evolution of a highland fauna only on Hispaniola, even though Jamaica reaches elevations where this fauna would otherwise occur. Island silhouettes represent the maximum elevation of each island, with species' elevational ranges in forested habitat represented by bars coming off the phylogeny (red, lowland species; blue, highland specialists). Nodes are colored according to likely ancestral state, with purple indicating greater uncertainty. (Left to right) Species associated with tree trunks on both islands: the Jamaican elevation generalist *Anolis opalinus*, the Hispaniolan highland-associated *Anolis christophei*, and the Hispaniolan lowland-associated *Anolis distichus*. (b,c) How local abundance and species richness on both islands decline as elevation increases. (b) When considering all species (solid lines), both islands have similar local anole abundances within 15-m-radius plots. But if highland species are discounted (i.e., only lowland species are counted; dashed lines), abundance trajectories diverge, with Hispaniola possessing far lower lizard densities at middle elevations in comparison to Jamaica. This difference between islands suggests that species from Jamaica's lowland fauna are maintaining relatively high abundances even at high elevations. (c) In contrast, when considering total species richness (solid lines), both islands have similar local diversity in the lowlands, but Hispaniola has many more species in local communities in the highlands. However, when discounting the evolution of unique highland species (i.e., lowland species only; dashed lines), species richness trajectories become similar between islands, suggesting that increased local diversity on Hispaniola is attributable to the evolution of its highland fauna. Taken together, these patterns indicate that in the lowlands, where area is sufficient for in situ speciation on both islands, community diversity converges. Yet local diversity diverges in the highlands, because limited area on Jamaica renders the highlands speciation limited and, therefore, local communities are depauperate. Despite differences in species richness, total abundance patterns within local communities are similar across islands, suggesting that communities on both islands are saturated in terms of individuals. (Left to right) Labels at the tips of the phylogeny indicate the first three letters of the corresponding species epithet: *A. opalinus*, *A. garmani*, *A. grabami*, *A. valencienni*, *A. lineatopus*, *A. reconditus*, *A. distichus*, *A. olsoni*, *A. semilineatus*, *A. etheridgei*, *A. insolitus*, *A. fowleri*, *A. christophei*, *A. baleatus*, *A. cybotes*, *A. callainus* (until recently *A. chlorocyanus*), and *A. aliniger*. Illustrations provided by Julie Johnson of Life Science Studios.

the predator (Lapiedra et al. 2018). In addition, this habitat switch brings *A. sagrei* into closer contact with more arboreal anole species, like *A. smaragdinus*, with which it is competitively dominant: On small experimental islands with all three species, populations of *A. smaragdinus* decline or are extirpated altogether (Pringle et al. 2019). Here, the mere threat of predation is sufficient to precipitate a behavioral shift in microhabitat use, which in turn destabilizes competitive interactions among anoles and drives local extinction (Figure 4).

By altering how organisms interact with their environments, behavioral changes—like habitat shifts in response to predation risk—can also influence the selective pressures that the organisms experience, potentially impacting evolution. A classic perspective is that behavioral shifts should prompt adaptive evolution: By introducing organisms to new resources or environments, changes in behavior should expose organisms to novel selective pressures and impel evolution (a concept known as behavioral drive) (Mayr 1963). As described above, the primary response of brown anoles to curly-tailed lizards is to abandon the ground for higher vegetation, as those predators are cumbersome climbers that infrequently venture into arboreal vegetation. While this arboreal shift limits predation risk, it also exposes brown anoles to selection on locomotor morphology: In the year following one experimental introduction of curly-tailed lizards, the switch to greater arboreality selected for reduced hindlimb length, presumably for greater agility on narrow branches (Losos et al. 2006) (Figure 4). Given the ubiquity of behavioral avoidance in the landscape of fear, evolution by behavioral drive may be an underappreciated catalyst of phenotypic diversity.

Conversely, behavior can constrain evolution. Through homeostatic behaviors like thermoregulation, organisms can select microhabitats to which they are already adapted, reducing exposure to selection and limiting evolution (a phenomenon known as behavioral inertia or the Bogert effect) (Huey et al. 2003, Muñoz 2022). Recent research on anoles highlights the retarding influence that thermoregulation exerts on physiological evolution. Daytime environments are thermally heterogeneous, facilitating thermoregulatory behavior and thereby slowing evolution of heat tolerance (Muñoz et al. 2014, Muñoz & Bodensteiner 2019). At night, by contrast, anoles are inactive and temperatures are homogeneous and cooler, limiting thermoregulatory opportunities. Anoles experience their warmest temperatures during the day and their coolest at night, while asleep.

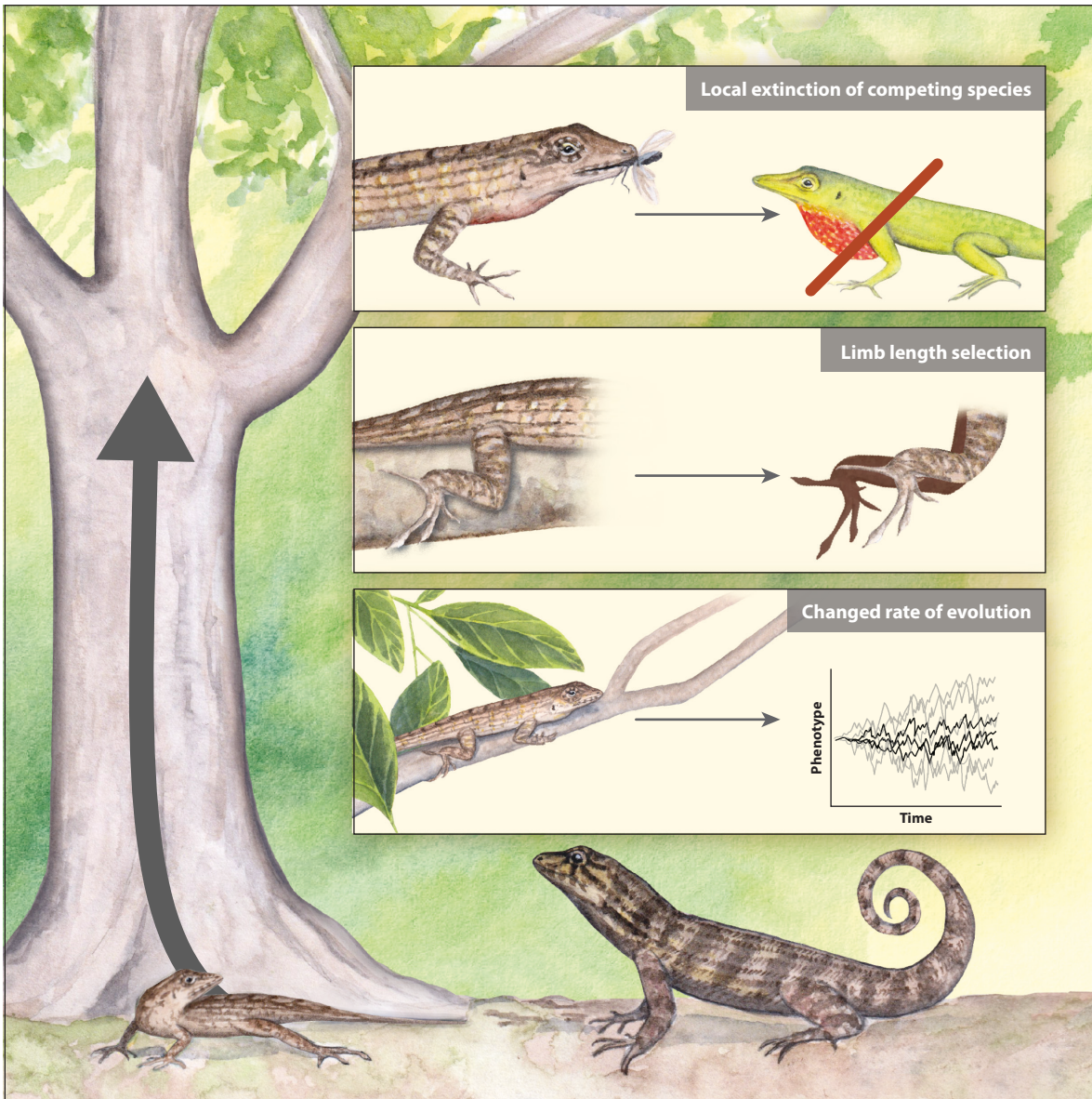


Figure 4

The landscape of fear alters anole ecology, community dynamics, and evolution. The presence of *Leiocephalus carinatus*, a predatory ground-dwelling lizard, pushes the trunk-ground anole *Anolis sagrei* into arboreal vegetation, promoting local extirpation of *A. smaragdinus*, an arboreal anole that competes for similar prey. On ecological timescales, shifts into arboreal habitat expose lizards to strong natural selection on limb length. Across macroevolutionary timescales, exposure to predators can hasten physiological evolution by limiting thermoregulatory behavior. Illustrations provided by Julie Johnson of Life Science Studios.

Without opportunities for behavioral thermoregulation at night, cold tolerance evolution vastly outpaces heat tolerance evolution (Muñoz et al. 2014, Muñoz & Bodensteiner 2019). In other words, only the aspects of physiology that behavior can buffer from selection exhibit a slowdown in evolution (Muñoz 2022).

Recent work with anoles provides new nuance to the Bogert effect, demonstrating that the relative strength of this phenomenon depends on the environmental context in which organisms operate (Muñoz 2022). In general, the Bogert effect is stronger when the costs of thermoregulation are low, such as when predation risk and distances among thermal patches are modest (Bodensteiner et al. 2021). Because island species, on average, thermoregulate more than mainland species, their rates of heat tolerance evolution are correspondingly slower (**Figure 4**) (Salazar et al. 2019). This thermoregulatory difference may, at least in part, reflect the fact that mainland anoles spend considerably less time moving around their environments than their island counterparts, perhaps due to stronger predation pressure (reviewed in Losos 2009).

Somewhat paradoxically, anoles reveal that behavioral drive and behavioral inertia can operate simultaneously (Muñoz & Losos 2018). This complex effect of behavior on evolution may unfold when a behavioral shift simultaneously influences selection along several phenotypic dimensions. Hispaniolan trunk-ground anoles (a lineage known as the cybotoids) diversified across elevation into distinct thermal habitats; nonetheless, their body temperatures remain largely unchanged across elevation due to thermoregulatory behavior. Whereas at low elevation *Anolis cybotes* mostly utilizes tree trunks in shaded habitats, at high elevation its close relatives *Anolis armouri* and *A. shrevei* instead perch on sun-soaked boulders (Muñoz et al. 2014, Muñoz & Losos 2018). This shift in microhabitat use confers thermoregulatory advantages, as boulders are more often optimally warm than arboreal perches at high elevations. While this behavioral shift shields montane anoles from selection on some aspects of physiology by limiting exposure to environmental extremes, it simultaneously drives morphological specialization for a boulder-dwelling lifestyle (Muñoz & Losos 2018). Given that any shift in resource use likely imposes multiple selective pressures, behavioral drive and inertia are intertwined, mutually dependent phenomena. In other words, homeostasis in one trait can be achieved only by “nonhomeostasis” in other traits (Lewontin 1983).

2.3. A Renewed Focus on Female Behavior Broadens Our Understanding of Anole Biology

Although *Anolis* lizards have long served as useful models in behavioral ecology, focus has centered on male behavior (Losos 2009). This lopsided perspective has yielded misapprehensions about the role of female behavior in *Anolis*. Historically, most anoles were characterized as exhibiting a polygynous mating system wherein territory-holding males seek exclusive mating access to resident females (reviewed in Kamath & Losos 2017). Yet, ongoing research emphasizes that females exert an underappreciated influence on mating outcomes. First, multiple paternity is common due to sperm storage and multiple mating (Calsbeek et al. 2007, Kamath & Losos 2018b). In addition, female anole territories often overlap with multiple males, including subordinate floater males, allowing access to multiple sires (Kamath & Losos 2018b, Johnson et al. 2021). Anoles also often leave their territories to access mates (Kamath & Losos 2018b). Together, these patterns suggest that exclusive polygyny, meaning that a single male maintains exclusive mating access to all of the females in its territory, may be relatively uncommon in anoles and that female behavior may play a greater role in mating than has traditionally been assumed (Kamath & Losos 2017, 2018a; Stamps 2018).

Conflicting perspectives surround the definition of anole territories and how territorial behavior translates into mating outcomes (discussed in Kamath & Losos 2017, 2018a; Bush & Simberloff 2018; Stamps 2018). Much of this debate centers on whether male territories grant exclusive access to females. Regardless, as in other vertebrate systems, the diverse territorial, aggressive, and sexual behaviors of females have been underexplored in anoles (Kamath & Losos 2017, Bush &



Simberloff 2018, Stamps 2018). With greater attention to female reproductive behavior, we can broach unanswered questions: Do trade-offs between territory size and encounter rates shape reproductive success in both males and females? How does pair bonding vary among anoles, and how does the spatial arrangement of territories of both sexes translate into reproductive outcomes (Johnson et al. 2021)? Why do females of some species have well-developed dewlaps, and in what contexts are they used (Harrison & Poe 2012, Yuan et al. 2022)?

Recent research has also focused greater attention on female nesting, an important but poorly understood dimension of anole ecology. For decades, our understanding of anole nesting was limited (reviewed in Pruett et al. 2022). Anoles' single-egg clutch and lack of nest guarding make nesting fast and inconspicuous, rendering it challenging to systematically observe. Additionally, most species' eggs are relatively small (<1 g), making them difficult to locate (but see Andrews & Rand 2022). Anole eggs can be found on the surface, underground, and even on cave walls, which long left unclear how effectively females selected nest sites for offspring fitness. Recent research indicates that female anoles successfully seek nest sites that enhance hatchling success (Pruett et al. 2022). In both field and laboratory-based studies, females seek out damp spaces, which provide conditions that improve offspring survivorship (Warner & Chapman 2011, Reedy et al. 2013). Females are also adept at nesting in cities, capitalizing on relatively cool and moist microsites like potted plants in landscapes otherwise unsuitable for laying eggs (Pruett et al. 2020, Tiatragul et al. 2020). Where optimal nest sites are limited, females can nest communally to capitalize on scarce nesting resources (Dees et al. 2020, Pruett et al. 2022). Taken together, these findings in anoles fit into an emerging consensus that nesting behavior in lizards is a key determinant of offspring survivorship and quality (reviewed in While et al. 2014).

3. EVOLUTIONARY BIOLOGY

3.1. Evolutionary Insights from Replicated, Seminatural Experiments

Around the turn of the last century, clever experiments on anoles living freely on small islands produced numerous influential insights, demonstrating that morphological evolution in natural populations could be both more rapid and more predictable than previously imagined (e.g., Losos et al. 1997). These experiments began a tradition of studying evolutionary processes in wild anole populations in real time that continues today. Recent research on free-living anoles has continued to illuminate the dynamics of selection and microevolutionary change, both revealing novel insights and clarifying or even qualifying some earlier conclusions.

Many such studies have broadened the phenotypic scope of earlier work, uncovering strong selection on physiological traits [e.g., thermal sensitivity of sprint speed (Logan et al. 2014), thermal tolerance (Campbell-Staton et al. 2017, 2021)] and behavioral traits [e.g., boldness (Lapiedra et al. 2018)]. Replicated microevolutionary studies have also shed light on the process of niche evolution during community assembly: Recent work on green (*A. carolinensis*) and brown (*A. sagrei*) anoles from Florida, for example, provided experimental evidence for evolutionary character displacement in the wild (Stuart et al. 2014), confirming a sometimes-disputed mechanism of evolutionary divergence that is often invoked but rarely rigorously tested (Stuart & Losos 2013).

While much of this work has focused on evolution by natural selection, replicated island systems have also been harnessed to explore less well-studied agents of evolution. The past century has seen critical debate over whether selection can overcome early imprints of founder effects—evolutionary changes resulting from an abrupt reduction in genetic diversity when populations are founded by small numbers of individuals or from subsequent genetic drift (evolution due to random sampling of alleles) as such populations evolve at very small size. Mayr (1963) argued that founder effects may impart lasting signatures on the genomes and phenotypes of populations,

altering future evolutionary trajectories. Alternatively, selection may be capable of rapidly eroding early imprints of founding genotypes and adaptively refining phenotypes (Barton et al. 1998, Schluter 2000). These contrasting ideas lingered untested for decades because of the inherent challenge of catching founding populations in the act. In an elegant study, Kolbe et al. (2012) experimentally transplanted single pairs of brown anoles from a common source population to a series of experimental founder islands. A strong founder effect initially followed introduction, as populations on experimental islands exhibited low allelic diversity and heterozygosity. This founder effect also shaped the phenotype, as experimental populations differed in relative hindlimb length, reflecting idiosyncratic sampling of source population diversity. Although adaptive evolution refined limb length over a few generations, founder effects of starting genotypes persisted. These experiments showed that while selection is a powerful evolutionary force, founder effects are similarly potent, imparting clear signatures on genetic and phenotypic diversity that can persist for at least several generations.

Similarly, new experimental research on Bahamian island anoles has also spurred a revision of past conclusions about the predictability of short-term evolutionary change. In a study investigating the ecological and evolutionary consequences of competition and predation, Thurman et al. (2023) found that short-term evolutionary outcomes were much harder to forecast than short-term ecological ones. In the 5 years following the experimental introduction of competitors (*A. smaragdinus*) and/or predators (*L. carinatus*) to small islands containing populations of brown anoles (*A. sagrei*), trajectories of phenotypic evolution in brown anoles could be predicted only for a limited set of traits, and patterns of genetic evolution were unpredictable. If generalizable (see discussion in Thurman et al. 2023), these results suggest that short-term evolution in response to complex species interactions may be less predictable than the repeated patterns of evolutionary change previously documented in anoles introduced to novel habitats (e.g., Losos et al. 1997, Kolbe et al. 2012). This lack of experimental evidence for repeatability in response to competition and predation is somewhat surprising, however, given the putative role of competition in spurring the repeated adaptive radiation of anoles into similar sets of ecomorphs on Greater Antillean islands (Williams 1983; Mahler et al. 2010, 2013). Resolving this mismatch across scales should be a priority for future research.

3.2. Comparative Insights Illuminate Deep-Time Evolutionary Patterns

Anolis research has contributed substantially to our understanding of macroevolution, as it has benefited from the spatial and phylogenetic replication this system provides: Geographically replicated anole radiations represent a macroevolutionary natural experiment. Crucial to such comparative investigation is sound knowledge of species diversity and its phylogenetic and biogeographic history. Recent years have seen tremendous progress in reconstructing the macroevolutionary history of anoles, by both novel sampling and species discovery, as well as the application of new techniques for phylogenetic and biogeographic analysis. In turn, a refined understanding of anole relationships has inspired new research on large-scale evolution in anoles.

Knowledge of the evolutionary history of *Anolis* has grown in several dimensions. Historically, taxonomic and phylogenetic work on Caribbean anoles dramatically outpaced work on mainland clades, although the latter contain most anole species (Nicholson et al. 2005). These long-overlooked continental clades have now received concentrated study that has clarified their composition and evolutionary relationships (del Rosario Castañeda & de Queiroz 2011, Prates et al. 2015). The last decade has also witnessed the first efforts to incorporate all recognized species of anoles within a single phylogenetic framework (Nicholson et al. 2012, Poe et al. 2017). Collectively, these efforts have made it possible to directly compare large-scale evolutionary patterns on the mainland and islands, revealing that mainland adaptive radiations can be just as ecologically



and phenotypically diverse as island ones but that these different geographic settings nonetheless result in the evolution of distinctive disparity patterns (e.g., Poe & Anderson 2019, Feiner et al. 2021, Huie et al. 2021, Patton et al. 2021).

In addition, taxonomic discovery has further illuminated several distinctive anole lineages during the last decade. For example, the unexpected discovery and subsequent phylogenetic analysis of a secretive giant anole on Hispaniola introduced a previously undocumented ecomorphological transition into the anole phylogeny (Mahler et al. 2016). Similarly, the discovery or rediscovery of several small montane species from eastern Brazil revealed an unexpected phylogenetic link between highland-dwelling anole clades occurring on opposite sides of the Amazon basin (Prates et al. 2017, Prates 2019). Expeditionary research clarified the relationships of two enigmatic species of horned anoles, now understood to be convergent in the possession of a fleshy rostral protuberance by males (Rodrigues et al. 2002, Yáñez-Muñoz et al. 2010), and has shown that the Mexican species *Anolis alvarezdeltoroi*, previously known from a single specimen, is a cave-dwelling karst specialist that resembles distantly related karst specialists from Cuba (Scarpetta et al. 2015). Simultaneously, paleontological discoveries offer a glimpse into the group's deeper evolutionary past. Most notably, a new trove of Dominican amber fossils confirms an ancient origin for several Hispaniolan anole ecomorph clades that persist today, implying faunal stability over epochal timescales (Sherratt et al. 2015).

New techniques for collecting and analyzing phylogenetic data have spurred advances in anole systematics, with some recent studies estimating phylogenies using genomic-scale data sets (Myers et al. 2021, Wogan et al. 2023). Phylogenomic studies of anoles have thus far focused primarily on relatively small subclades, and we eagerly anticipate the application of such approaches at larger scales in *Anolis*, as recently seen in other iconic radiations such as passerine birds (Prum et al. 2015). An encouraging outcome of most recent phylogenetic work is that traditional phylogenetic analyses largely agree about the membership of major anole clades, suggesting an emerging consensus on key aspects of the group's phylogenetic diversity (Nicholson et al. 2012, Poe et al. 2017). For example, recent studies show consensus for a Caribbean origin of the clade containing most extant mainland anole species (the *Draconura* clade) (**Figure 1**) and confirm that Greater Antillean anole diversity is overwhelmingly the product of within-island diversification. Nonetheless, there is topological discordance between different phylogenetic markers in some anole clades (Mahler et al. 2016, Myers et al. 2021, Wogan et al. 2023). Because hybridization appears relatively uncommon in anoles (reviewed in Losos 2009), conventional wisdom has been to assume that such discordance, where it occurs, is the result of differences between the evolutionary histories of species and of their genes (e.g., due to incomplete lineage sorting). Recent research on Jamaican and Puerto Rican anoles, however, suggests that at least some detected genealogical discordance may stem from ancient hybridization during these insular radiations (Myers et al. 2021, Wogan et al. 2023), a tantalizing possibility that could reshape our understanding of the origins of anole diversity. For example, the introgression detected in Puerto Rican anoles is inferred to have occurred between lineages that now differ greatly in ecomorphology (e.g., between the recent ancestors of the trunk-ground anole *Anolis cristatellus* and the grass-bush anole *Anolis pulchellus*), and comparative analyses support a model in which hybridization led to transgressive trait evolution [i.e., an evolutionary scenario in which a hybrid lineage exhibits trait values outside the range observed in its parent lineages (Wogan et al. 2023)].

3.3. Repeatability Is Common in Macroevolution but Not Universal

Improved knowledge of anole phylogenetic history has shed light on one of biology's most enduring questions: Can evolution produce predictable outcomes over vast periods of time, or do chance events and contingencies render macroevolutionary convergence uncommon (Gould

1989)? Although the striking convergence of ecomorphs across the Greater Antilles has long been recognized (Williams 1983), roughly one-fifth of anole species from these islands are not easily assignable to a convergent ecomorph class (Losos 2009), and these species were excluded from past studies of convergence. Truly testing whether macroevolution is repeatable requires assessing the frequency of convergence across entire radiations, including species that may not be convergent, since diverse evolutionary radiations can produce substantial evolutionary convergence due to chance alone (Stayton 2006).

Using an analytical approach inspired by Simpson's (1953) concept of the adaptive landscape, Mahler et al. (2013) found that entire radiations of Greater Antillean anoles exhibited substantially more convergence than expected by chance in traits associated with microhabitat specialization, even though evolution also produced many nonconvergent lineages on these islands. Frequent convergence between anoles from different islands, often radiating millions of years apart, suggests that aspects of the macroevolutionary adaptive landscape can be stable across space and time (Mahler et al. 2013). Furthermore, the exploration of such landscapes by radiating lineages appears to be limited by island area and topographic complexity (Mahler et al. 2013), factors required to transform available ecological opportunities into evolutionary opportunities for diversifying clades (Frishkoff et al. 2022). Exceptional ecomorphological convergence in Greater Antillean anoles has since been corroborated by studies incorporating additional measurements of locomotor morphology (Tinius et al. 2018, 2020; Feiner et al. 2020). The quantitative approaches pioneered in research on anoles have also been used to examine convergence in dozens of other systems. A key emerging insight is that macroevolutionary convergence is more common than previously appreciated, with exceptional levels of among-clade convergence observed even between radiations that last shared a common ancestor in the Mesozoic [e.g., in pythons and boas (Esquerré & Keogh 2016)]. Accordingly, anole researchers have begun to direct their attention to increasingly deeper evolutionary timescales, asking whether replicated evolutionary patterns detected within *Anolis* are also matched in more distantly related radiations of lizards, such as geckos or gliding dragons (Ord et al. 2015, 2021; Hagey et al. 2017).

Research on *Anolis* is also reshaping our understanding of when and where striking convergence may be expected to evolve. Historically, iterated ecomorphological convergence had been assumed to occur predominantly among the endemic biotas of islands and lakes due to the relative ecological simplicity of those habitats (Schluter 2000, Stroud & Losos 2016). Recent discoveries of extensive convergence involving continental anole faunas have begun to overturn this notion: *Anolis*-wide investigations have revealed convergence between mainland groups, and they have yielded some evidence for convergence between insular and continental radiations (Moreno-Arias & Calderón-Espinosa 2016, Poe & Anderson 2019, Huie et al. 2021, Patton et al. 2021). Perhaps most surprising is that convergence appears to be no less common on the mainland than in the Greater Antilles (Poe & Anderson 2019). What remains unclear is why some anole phenotypes have evolved in both mainland and island settings [e.g., twig-ecomorph anoles and members of the recently proposed ground ecomorph (Losos et al. 2012, Prates et al. 2017, Huie et al. 2021)], while the convergent evolution of others has been limited to either insular or continental settings [e.g., large crown-dwelling anoles converge to one morphology in the Caribbean but to another in the Neotropical mainland (Poe & Anderson 2019)]. This patchwork pattern of similarities and differences gives credence to the notion, often attributed to Mark Twain, that "history doesn't repeat itself, but it often rhymes." Understanding this partial convergence will require more detailed studies of mainland anole community ecology and performance, topics for which knowledge of mainland species still lags behind that of Caribbean species, but for which early work suggests there are important differences (Andrews 1979). Regardless, the expanded evidence for the emergence of repeated evolutionary motifs across both mainland and island anole radiations suggests



we may need to reassess the idea that macroevolutionary convergence should be most common in simple, competition-structured ecological settings (Poe & Anderson 2019, Patton et al. 2021).

Complementary insights into convergent evolution have emerged from a dramatic expansion of phylogenetic comparative investigation to examine scalation, claw morphology, physiology, display behavior, and diving (Muñoz et al. 2014, Wegener et al. 2014, Gunderson et al. 2018, Salazar et al. 2019, Yuan et al. 2019, Baeckens et al. 2021, Boccia et al. 2021, Ord et al. 2021). Such work revealed iterated convergence in a remarkable behavior that had gone unnoticed by earlier generations of anole biologists—underwater rebreathing in semiaquatic anoles (Boccia et al. 2021) (Figure 5). Certain anoles regularly dive into streams to escape predators and, while submerged,

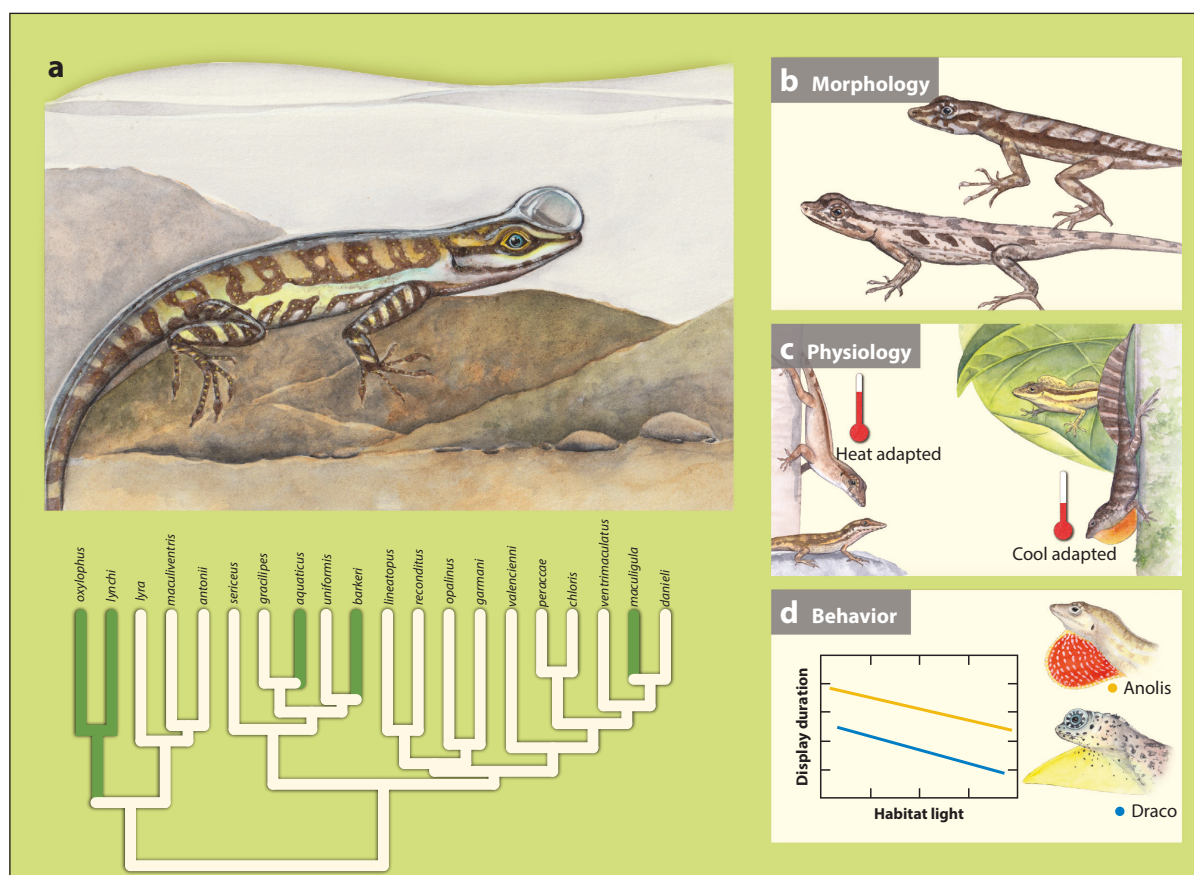


Figure 5

Multiple dimensions of convergence in *Anolis* lizards. (a) Aquatic anoles (illustrated here by *Anolis aquaticus*) represent a remarkable case of behavioral convergence involving the use of rebreathing bubbles for diving. Green lines on the phylogeny indicate four independent origins of this phenomenon (two additional origins are not shown). (b) Testing for morphological convergence across all anoles reveals a greater diversity of replicated convergence in morphology between mainland and island anoles than previously expected, illustrated here by the convergent similarity of the ground-dwelling *A. barbouri* from Hispaniola and *A. humilis* from Central America. (c) Morphologically dissimilar species of anole often converge in ecophysiology, with some species exhibiting a warm-adapted ecophysiology (e.g., *A. cristatellus*, *A. poncensis*) and others exhibiting a cool-adapted ecophysiology (e.g., *A. krugi*, *A. gundlachi*). (d) Expanding beyond anoles, we discover that anole display characteristics are convergent with *Draco* lizards, specifically in the use of dewlaps for social communication and in the relationship between ambient light and dewlap duration. Illustrations provided by Julie Johnson of Life Science Studios.

continue to breathe by exhaling air into a bubble that forms on the skin and then reinhaling it (similar to the rebreathing mechanism of some diving arthropods). A striking element of this discovery is that this highly stereotyped rebreathing behavior, which thus far appears to be unique among vertebrates, arose at least six times in anoles (Boccia et al. 2021) (**Figure 5**). Field experiments and phylogenetic analyses suggest that the key to this replicated evolutionary adaptation lies in the hydrophobic skin possessed by all anoles, which likely served as an exaptation for evolving rebreathing (Boccia et al. 2021).

In addition to ecomorphology and behavior, Caribbean anoles have converged in thermal ecology and in physiological specialization. Once ecomorphs arise, they often proliferate into endemic radiations with up to a dozen species. Within-ecomorph divergence often involves specialization in ecophysiology to distinct microclimatic niches. On Jamaica and Puerto Rico, for example, species vary in their use of open or edge habitats (warm niche) and closed-canopy habitats (cool niche) (Gunderson et al. 2018). Changes in habitat preference have repeatedly evolved in anole lineages on these islands, such that close relatives often exhibit little overlap in thermal habitat use (Gunderson et al. 2018). Such shifts in thermal habitat use are associated with physiological specialization: Warm-niche species tend to have higher optimal sprinting temperatures and are more heat tolerant than their cool-niche counterparts (Gunderson et al. 2018) (**Figure 5**). Yet, these same patterns do not emerge in Hispaniola. On this large, topographically complex island, close relatives tend to be separated allopatrically across biogeographic boundaries and do not diverge in their heat tolerance or thermal habitat preferences (Muñoz et al. 2014). Some close relatives are parapatrically separated across elevations and, in these cases, diverge only in cold tolerance (Muñoz et al. 2014). Thus, just as most of the Greater Antilles have species that are morphologically unmatched on other islands, despite morphological convergence being exceptionally common [e.g., the Hispaniolan leaf-litter specialist *Anolis barbouri* has no analogue on the other three Greater Antillean islands (Losos 2009)], ecophysiology exhibits strong parallels across islands, as well as key points of divergence. Evolutionary patterns of ecomorphology and ecophysiology indicate that determinism and contingency both shape the evolution of island faunas. Although we lack a firm understanding of the factors that promote convergence in some cases and divergence in others, island size, topographic complexity, historical biogeography, and occupancy time are promising candidates for future investigation.

Phylogenetic studies of anoles have also raised new questions about the factors that influence the tempo of macroevolution. According to the ecological theory of adaptive radiation, ecological opportunity—defined as the ecological availability of evolutionarily accessible resources—is key in determining the rate of phenotypic evolution during diversification (Schluter 2000, Stroud & Losos 2016). Recent research on anoles provides mixed support for this hypothesis. Ecological opportunity is generally assumed to be greater in insular settings compared with continental ones, especially when islands are relatively young and unsaturated (Schluter 2000). Somewhat surprisingly, then, rates of ecomorphological evolution are in fact equivalent between mainland and island anoles (Pinto et al. 2008, Burrell & Muñoz 2022; but see Feiner et al. 2021), suggesting that the rate of phenotypic evolution is determined less by competing lineages than by other factors. Indeed, some have suggested that the evolution of adhesive toe pads—an innovation that endowed anoles with access to a diversity of arboreal microhabitats—may represent a more consequential source of ecological opportunity for adaptive radiation in anoles than release from competing lineages on islands (Miller & Stroud 2021, Burrell & Muñoz 2022). Other research, however, suggests that the rate of phenotypic evolution may indeed be coupled to the accumulated diversity of competing lineages (Mahler et al. 2010, Drury et al. 2016) and potentially to secondary contact among long-separated lineages (Patton et al. 2021). These alternative conclusions may stem from disparate approaches for quantifying ecological opportunity and invite further study.



3.4. Bridging Micro- and Macroevolutionary Studies in *Anolis* Lizards

Much of the value of the *Anolis* system for evolutionary study derives from its natural replication across space and time. At the microevolutionary scale, such replication largely relies on the independent experimental units afforded by small islands. At macroevolutionary scales, replication occurs at deeper timescales and across biogeographic regions, resulting in repeated bouts of speciation and specialization. While both micro- and macroevolutionary studies of anoles generate new insights, these lines of inquiry mostly operate independently: Studies bridging microevolutionary processes with macroevolutionary phenomena remain a persistent gap in the literature.

To better understand how evolutionary forces (e.g., selection and constraint) produce broad-scale patterns (e.g., ecomorphological diversity) we need to better connect genetic variation to phenotypic change. Understanding the genetic architecture of traits provides such a connection. The evolution of genetic architecture can be investigated indirectly through the genetic-covariance structure of multivariate trait variation, known as the G matrix (Lande 1979, Arnold et al. 2001). In theory, the G matrix may evolve convergently if it responds in the same way to similar selective pressures. In research on distantly related yet phenotypically convergent anole species representing three different ecomorphs, however, G matrices exhibited overwhelming stability among species separated by >40 million years, reflecting deep conservation of evolution along genetic lines of least resistance (McGlothlin et al. 2018, 2022). Nonetheless, some aspects of genetic covariation did exhibit signals of convergence among some anole taxa, suggesting that the power of constraint is not unyielding and that selection can drive adaptive evolution in the G matrix. In a manner analogous to phenotypic evolution (Section 3.3), the evolution of genetic architecture reflects an interplay between selection and history (McGlothlin et al. 2022).

Landscape genetic approaches offer another bridge between micro- and macroevolutionary scales. Such approaches aim to identify the geographic and environmental features influencing gene flow, mechanistically linking proximate correlates of local adaptation to population divergence and speciation. Geographic distance exerts a stronger influence on Caribbean anole genetic structure than environmental difference (Wang et al. 2013), consistent with the notion that large geographic areas are required to transform ecological opportunity into high species richness (Losos & Schluter 2000, Frishkoff et al. 2022).

In addition to genetic approaches, long-term experiments may furnish unique microevolutionary insights. For example, microevolutionary studies in anoles are largely restricted to a handful of generations, across which directional evolution is evident. It is less clear how the arc of evolution bends over intermediate timescales. Longer-term monitoring of microevolutionary systems, natural or seminatural, would help bridge this gap. Likewise, while the effect of ecological change on evolution has been studied for decades, the inverse—how evolutionary change influences ecological dynamics—has received considerably less attention (Schoener et al. 2017).

4. ANOLIS ANTHROPOCENE BIOLOGY

4.1. Rapid Evolution in Response to Ongoing Environmental Change

Anoles are emerging as a powerful source of insight into how biological systems are likely to respond to human actions. Much of this work rests on seminal research conducted during the 1990s, which established *Anolis* as a model system of rapid evolution (Losos et al. 1997). The growing recognition that phenotypic evolution can be observed over very short timescales inspired efforts to test whether anoles have undergone adaptive evolution in response to stressful conditions precipitated by human activities. So far, inquiry has focused on extreme climatic events with an eye toward future climate change, human-mediated introductions of species to novel environments,

and urbanization as a particularly severe form of land-use change. These efforts have uncovered abundant evidence of physiological and morphological evolution following anthropogenic change.

Despite their short duration, extreme climate events may have marked evolutionary outcomes. In 2014, an intense winter storm across the United States imposed strong selection that resulted in a rapid increase in cold tolerance in the southernmost populations of the green anole, *A. carolinensis*. Furthermore, these southern populations underwent a shift in gene expression that recapitulated preexisting patterns observed in northerly populations that more frequently experience cold temperatures (Campbell-Staton et al. 2017).

Species introductions also expose organisms to novel selection. Invasion of the Cuban *A. sagrei* in the southern United States, where it interacts with native *A. carolinensis*, has helped reveal the evolutionary signatures of invasion. *A. carolinensis* move to higher perches to avoid interactions with the more terrestrial brown anole, *A. sagrei*, and evolve larger toe pads and more lamellae in only tens of generations, presumably to optimize performance in more arboreal settings (Stuart et al. 2014). Similar phenomena occur in places where anoles are introduced to species-poor communities. The Puerto Rican crested anole, *A. cristatellus*, has recently invaded the small island of Dominica, triggering a similar upward habitat shift in native *Anolis oculatus*. Where sympatric, *A. oculatus* perches higher and has evolved shorter limbs, an adaptation facilitating clinging to narrow surfaces. The invading *A. cristatellus* has done the opposite, evolving longer limbs (Dufour et al. 2017). Morphological adaptations to readily partitioned structural habitat may be one of the most common evolutionary responses to anthropogenic species introductions.

Lastly, urban environments are fertile ground in which to investigate adaptive evolution to anthropogenic change. Such adaptation is likely to be multipronged: Land-use change simultaneously alters resource availability, modifies habitat structure, and changes climate, usually by increasing temperature and decreasing humidity (although irrigation in arid regions can increase humidity relative to natural environments). *A. cristatellus* has so far been the best-studied anole system for urban adaptation. In response to the heat island effect, urban populations of this species exhibit the ability to withstand hot temperatures. Such heat resistance is matched by genetic signatures of selection: consistent sequence divergence between urban and forest populations across Puerto Rico in the protein-synthesis gene *RARS*, as well as across hundreds of other genes for which expression levels differ when exposed to urban-like temperatures (Campbell-Staton et al. 2020) (**Figure 6**). In part, these genetic differences in urban populations arise via the purging of alleles that generate maladaptive responses to heat stress (i.e., cases in which expression decreases thermal tolerance in response to chronic heat exposure). Such alleles are relatively common in forest populations, presumably because infrequent exposure to heat stress is permissive to a higher genetic burden (Campbell-Staton et al. 2021). Not only are urban environments warmer but also their largely artificial perches are typically broader and smoother than the arboreal substrates of natural environments. Accordingly, urban lizards have evolved longer limbs and more lamellae than their forest-dwelling counterparts (Winchell et al. 2016), which facilitate grip and allow them to run rapidly and nimbly on broad, smooth surfaces (Winchell et al. 2018) (**Figure 6**).

4.2. The Anthropocene Is Reorganizing Biodiversity Patterns

The diversity of *Anolis*, its broad geographic range, and the existence of near-complete phylogenies (Poe et al. 2017) make it a good system for understanding how anthropogenic change is reorganizing Earth's biodiversity. Despite the evolutionary novelty of many human threats, anole responses tend to be phylogenetically clustered, with close relatives more likely to tolerate urbanization (Winchell et al. 2020) or establish outside their native range (Latella et al. 2011). This suggests that a constellation of phylogenetically conserved traits determine success in the Anthropocene.



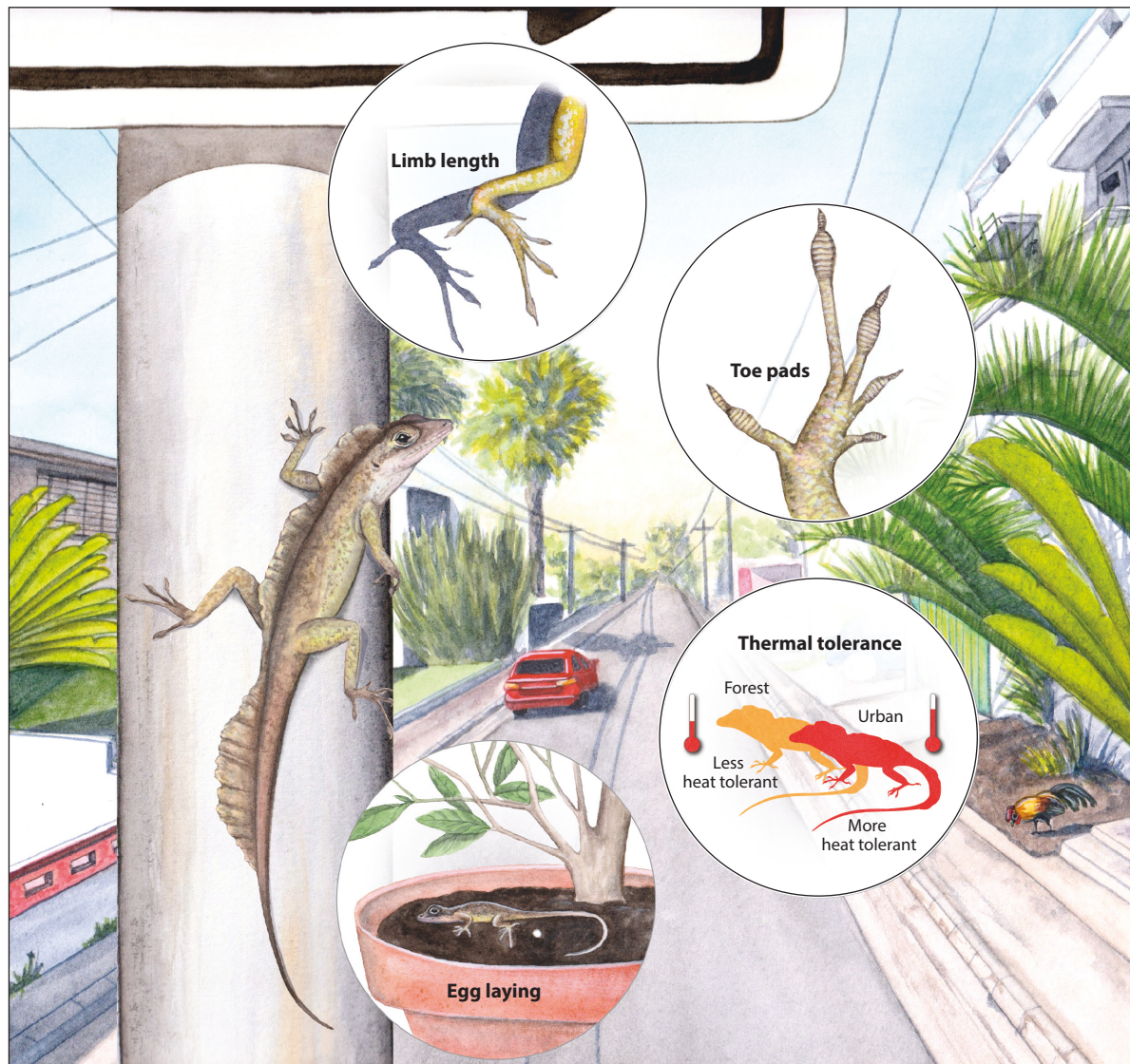


Figure 6

Anoles such as *Anolis cristatellus* that thrive in urban areas display morphological and physiological adaptations, as well as plasticity and behavioral strategies in nesting behavior to cope with harsh conditions and limited habitat. These responses include lengthening limbs and expanding toe pads to permit better gripping on smooth and wide human-made surfaces, as well as increasing heat tolerance to survive hot city conditions [indicated by the higher upper thermal limit for locomotion for urban anoles (*red*) relative to nonurban anoles (*orange*)]. Urban anoles adeptly seek out sites amenable for egg laying, such as in potted plants. Illustrations provided by Julie Johnson of Life Science Studios.

The frequency of anole invasions has illustrated how human actions are recasting biogeography and changing the factors that control species richness. Historically, and as predicted by the theory of island biogeography (MacArthur & Wilson 1967), anole species richness on islands is a function of both island area and geographic isolation. Native anole faunas on isolated islands thus tend to be undersaturated, with fewer species than would be predicted from area alone. Presumably these

environments could support more species if colonization or in situ speciation were not limiting. Beginning with the sharp uptick in international trade following World War II, the rate of anole introductions has accelerated throughout the twentieth century to the present day (Helmus et al. 2014). Transoceanic trade can permanently move anole-containing cargo to new locations and is the primary cause of anole species introductions. These introductions have been especially successful on undersaturated islands, resulting in geographic isolation becoming progressively less important in determining species richness, while the effect of island area has become more deterministic (Helmus et al. 2014). Despite this anthropogenic increase in island-level diversity, invaded anole communities do not appear to differ from similar-sized natural communities in morphological structure, suggesting that the ecological filters that determine establishment success operate in similar ways regardless of whether communities obtain species through anthropogenic or nonanthropogenic means (Poe 2014).

Land-use changes have likewise reshaped patterns of diversity in unexpected ways. On Hispaniola, replacement of forest by cattle pastures, coffee plantations, and other forms of agriculture has decreased anole abundance but has left local-community species richness values unchanged. Instead of species losses, these land-use changes have reshuffled the geographic organization of communities: Endemic species in highland communities are unable to persist after deforestation, but the ensemble of lowland species tolerate deforestation quite well. Species that are affiliated primarily with lowland forests also now occur at high elevations in deforested areas, at the expense of the endemic highland forest community (Frishkoff et al. 2019). Even where species ensembles persist in human-modified habitats, different species use these novel habitats in starkly divergent ways. Some species like the Puerto Rican *Anolis stratulus* tolerate urban areas well but restrict their microhabitat use to remnant vegetation like solitary trees or planted bushes. In contrast, *A. cristatellus* commonly exploits anthropogenic microhabitats such as buildings and, perhaps as a result, reaches proportionally higher abundances in urban settings (Winchell et al. 2018). While the preponderance of research identifies the costs to organisms of human-modified habitats, certain species are poised to benefit from novel resources available in these settings. Artificial nighttime lighting concentrates insect prey and can extend the activity time of diurnal insectivores like anoles. When exposed to such lighting, *A. sagrei* grows more quickly and has a higher reproductive output (Thawley & Kolbe 2020). Different intrinsic capacities to benefit from such ecologically and evolutionarily novel opportunities, in addition to simply withstanding them, likely play a crucial role in separating Anthropocene winners from tolerators from losers. So far, we lack a coherent ecological theory to predict when a species will be able to exploit these new resources, but anoles may represent a powerful system to develop and test such hypotheses.

Empirically, however, one attribute does tend to predict winners. Warm- and xeric-adapted lowland species tend to thrive under anthropogenic biodiversity reorganization, while cool, mesic-adapted species tend to be most threatened by anthropogenic change. Indeed lowland species, like the frequent invaders *A. sagrei* and *A. cristatellus*, are predisposed to succeed after anthropogenic introduction to new areas (Latella et al. 2011), potentially because they have intrinsic characteristics (e.g., greater heat tolerance) that allow them to survive as stowaways in transoceanic cargo. Moreover, lowland species are more likely to occur at ports, which furnish opportunities for accidental transport, and are also preadapted to their likely destinations of other lowland port cities. Warm-adapted lowland anoles also appear best positioned to tolerate both deforestation and urbanization (Frishkoff et al. 2019, Winchell et al. 2020), likely because occurrence in the lowlands adapts them to warm conditions generally and preadapts them to survive the up-to-10°C increase in local temperatures after thermally buffering forest canopies are eliminated. As discussed above, these warm-adapted lowland species can even invade deforested habitats at high elevations where they do not occur in natural forests (Frishkoff et al. 2019). This same logic can be used to predict



the responses of anole populations and species to climate warming. Islands of the Caribbean are predicted to become warmer and drier, likely favoring warm-adapted and xeric species (Thonis & Lister 2019) and perhaps allowing them to expand upslope at the expense of highland species.

5. ONGOING EVOLUTION OF THE ANOLE MODEL SYSTEM

Contemporary research on *Anolis* ecology and evolution has harnessed decades of foundational work to advance—or even reframe—our fundamental understanding of community assembly, microevolution, and adaptive radiation. This foundation likewise provided a set of core hypotheses that helped establish anoles as a tractable system for Anthropocene biology. One could imagine that, with decades of exploration and growth, *Anolis* has reached its empirical and conceptual apotheosis. On the contrary, we argue that anoles are better suited than ever for deeper and broader inquiry. Recent research on anoles shows that continued intensive investigation of a model system can refine long-standing ideas as classic hypotheses are reevaluated with fresh perspectives (e.g., Kamath & Losos 2017, Muñoz & Losos 2018, Pringle et al. 2019). Such study can also open up entirely new frontiers of inquiry, both from new natural history discoveries (e.g., Prates et al. 2017, Boccia et al. 2021) and from the application of newly developed scientific techniques (e.g., Myers et al. 2021, Winchell et al. 2023, Wogan et al. 2023). The study of anoles continues to be both integrative, as the system is approached from multiple disciplinary angles, and hierarchical, uniting information from molecules to ecosystems. These features helped make anoles a powerful model system for ecology and evolution and will continue to propel further inquiry. As is true for any system that cumulatively builds biological insight, greater knowledge only urges further discovery.

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