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Experimentally simulating the evolution-to-ecology connection: Divergent predator morphologies alter natural food webs

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The idea that changing environmental conditions drive adaptive evolution is a pillar of evolutionary ecology. But, the opposite—that adaptive evolution alters ecological processes—has received far less attention yet is critical for eco-evolutionary dynamics. We assessed the ecological impact of divergent values in a key adaptive trait using 16 populations of the brown anole lizard (*Anolis sagrei*). Mirroring natural variation, we established islands with short- or long-limbed lizards at both low and high densities. We then monitored changes in lower trophic levels, finding that on islands with a high density of short-limbed lizards, web-spider densities decreased and plants grew more via an indirect positive effect, likely through an herbivore-mediated trophic cascade. Our experiment provides strong support for evolution-to-ecology connections in nature, likely closing an otherwise well-characterized eco-evolutionary feedback loop.

Anolis | eco-evolutionary dynamics | evolution-to-ecology connection | trophic cascade

With the title of his volume "The Ecological Theater and the Evolutionary Play," Hutchison (1) eloquently captured the thrust of classic evolutionary ecology—the ecological environment sets the stage for adaptive evolution. Landmark studies of beak size in Darwin's finches (2), age at maturity in Trinidadian guppies (3), and limb length in Caribbean anoles (4) demonstrate this ecology-to-evolution connection on contemporary timescales. Our understanding of how ecology affects evolution has since grown expansively, especially as studies document evolutionary responses to rapid environmental change caused by humans (5–8). With recognition of the widespread potential for rapid adaptation (9, 10) and the development of eco-evolutionary dynamics (11–15), attention has turned to studying the inverse scenario—can rapid phenotypic evolution alter species interactions or ecosystem function? Over the last decade, laboratory and mesocosm experiments have probed this evolution-to-ecology connection, showing that intraspecific trait variation results in differential effects on food webs and ecosystems (e.g., refs. 16–22). However, it remains unclear whether the effects of trait evolution on ecological interactions illustrated in these small-scale studies manifest in complex natural ecosystems. Establishing such connections is necessary for closing eco-evolutionary feedback loops, a needed step for advancing the field of eco-evolutionary dynamics (14).

Background on Our Bahamian Island Study System

To study the evolution-to-ecology connection in nature, we capitalized on decades of research on adaptive trait evolution and food web interactions in small-island ecosystems in the Bahamas. We established experimental populations of a generalist predator that differed in a rapidly evolving trait linked to foraging and evaluated the effects on lower trophic levels. Specifically, we introduced brown anole lizards (*Anolis sagrei*) that varied in limb length, a well-studied adaptive trait with a strong functional relationship with locomotion related to the vegetative habitat (23). Previous experiments show that brown anole limb length is under selection (24, 25) and populations adapt rapidly to the narrow, scrubby vegetation on small islands, which favor lizards with shorter limbs (Fig. 1*A*, 4, 26). Moderate heritability (27) and a large-effect locus (28) for limb length variation in brown anoles indicate available genetic variation and a genetic architecture amenable to an evolutionary response to selection. Brown anoles also have strong top-down effects on island food webs, including mainly direct effects on prey such as spiders (e.g., ref. 29) and indirect effects on plants through a trophic cascade (e.g., refs. 30 and 31). Thus, we can simulate evolution of a key adaptive trait in a top predator and quantify the cascading effects through a well-characterized food web. We have a deep understanding of the adaptive significance and evolutionary dynamics of limb length in brown anoles, yet until the present study, we did not know whether limb variation had any ecological consequences.

Significance

Eco-evolutionary dynamics capture the reciprocal feedback of ecological and evolutionary processes on contemporary timescales. Rapid adaptation in response to environmental change is well documented, but we lack an understanding of how evolved trait values affect ecological processes in natural systems—that is, evolution-to-ecology connections. Using islands as replicated experimental units, we demonstrate that adaptive variation in lizard limb length dramatically affects ecosystem structure—specifically, short-limbed lizards enhance plant growth. Our findings aid in closing an otherwise well-supported eco-evolutionary feedback loop wherein lizard limb length adaptively responds to vegetation structure and plant growth is influenced by lizard limb length mediated through food web interactions. Our results provide unprecedented support for evolution-to-ecology connections in nature, verifying a key prediction for eco-evolutionary dynamics.

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The authors declare no competing interest.

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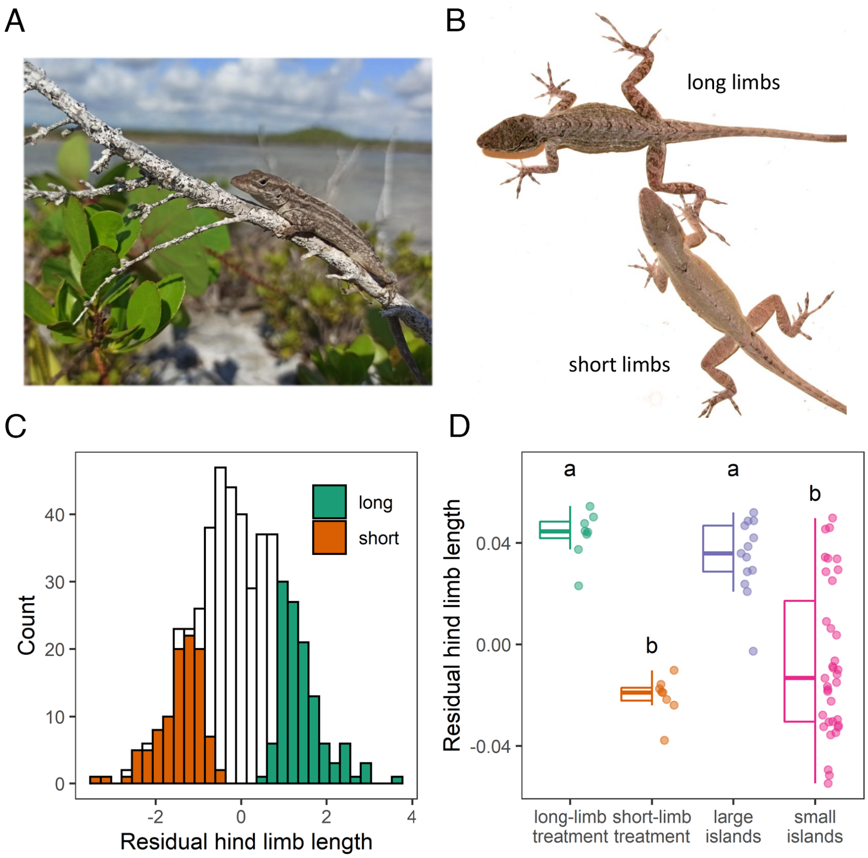

Fig. 1. Brown anole limb-length variation in experimental treatments and compared to natural island populations in the Bahamas. (*A*) Adult male brown anole (*A. sagrei*) perched in a typical position on vegetation from an island in our experiment. (*B*) Two of the lizards used in the island experiment; both lizards have the same snout-vent length (SVL = 54 mm), but one is from the long-limbed treatment (hindlimb length = 42.5 mm) and the other is from the short-limbed treatment (hindlimb length = 36.5 mm). These extreme trait values correspond to an ~15% difference in hindlimb length. The average difference in relative hindlimb length between long- and short-limbed treatments was 7.1%. (*C*) Histogram of limb lengths for lizards captured for this study (all bars; total of 488 lizards) and those introduced to islands for the experiment (filled bars; 118 long-limbed lizards and 102 short-limbed lizards). (*D*) Limb lengths of lizards used in the island experiment (n = 8 islands per limb-length treatment) and in naturally occurring populations on large islands (n = 13) and small islands (n = 35) throughout the Bahamas; island-level mean limb lengths are shown. Letters indicate statistically significant differences based on post-hoc Tukey's tests from models described in the *Methods*. Residual hindlimb lengths are from regressions of ln[hindlimb length] on ln[SVL]. Photo credits are O. Lapiedra for panel *A* and S. Giery for panel *B*.

Predictions for the Effect of Brown Anole Limb Length on Food Web Interactions

From a locomotor performance perspective, we can predict how limb-length variation in brown anoles will influence their habitat use and foraging ability in small-island habitats and consequently alter their top-down effects on island food webs. Shorter-limbed brown anoles maneuver more effectively on thinner-diameter vegetation (23, 32), which is the dominant size of vegetation on the small islands in our study (26). Moreover, previous studies show that anoles selectively occupy perches that enhance their locomotor performance (33, 34), meaning that brown anoles may both selectively occupy and perform better in habitats that match their limb length. Thus, we can generate clear predictions for how small-island habitats favor brown anoles with short limbs and how predators with these traits will directly and indirectly affect food webs. Lizards with short legs are predicted to be more effective foragers in arboreal habitats, leading to stronger negative effects on arboreal prey such as web spiders, weaker effects on more ground-based prey such as salticid spiders, and stronger indirect positive effects on plants via their negative effects on herbivorous arthropods. A previous experiment in this system found that web spiders had no significant effect on plants (35); thus, we expect stronger effects of lizards on plants through a three-level lizard–herbivore–plant trophic cascade. Finding that differences in limb length of a top predator alter underlying food web interactions on real islands would provide strong experimental evidence for an evolution-to-ecology connection, and the reciprocal effects of evolution and ecology would support the importance of eco-evolutionary dynamics in nature. Such effects are potentially widespread because brown anoles vary extensively in limb length among populations throughout their range (36) and are known to have large, multilevel effects on food webs (29–31). These attributes make the brown anole and our Bahamian study system excellent for an eco-evolutionary study to detect the effects of limb length evolution on food webs.

Overview of the Experimental Design

To produce short- and long-limbed experimental populations, we captured 488 adult male brown anoles from mainland Great Abaco and measured their body size (i.e., SVL) and hindlimb length. We individually tagged and translocated the 220 lizards with the relatively shortest and longest hindlimbs (based on the tails of the relative hindlimb length distribution, Figs. 1 *B* and *C*) onto 16 lizard-free small islands, which serve as replicated, whole-ecosystem experimental units (24–26). This manipulation resulted in islands occupied by lizards in two classes, either short or long legs (*SI Appendix*, Table S1). Our short- and long-limbed treatments closely matched limb length differences for brown anoles found naturally on small and large islands, respectively, throughout the Bahamas (based on data from 912 male lizards collected over a 17-y period on 48 islands, Fig. 1*D*). Our manipulation resulted in an average hindlimb length difference between treatments of 7.1% when accounting for body size (*SI Appendix*, Fig. S1). Because changes in trait values and densities are often confounded in comparative studies of natural populations and many experimental treatments, we crossed our limb-length treatment with a density treatment. This allowed us to evaluate the individual and interactive effects of limb length and density, providing insight into the context in which evolution-to-ecology effects are realized in nature. We used high and low densities derived from annual density estimates for 24 island populations over a 9-y period. Thus, our long-term data on brown anole morphology (4, 26, 36–37) and population density (37) allow us to use ecologically realistic values for our experimental treatments. We used only adult male lizards to prevent changes in limb length and density due to reproduction because female brown anoles can produce viable eggs from stored sperm for multiple months (38). We collected pretreatment food web data on spider abundance, plant growth, and leaf damage in May and September 2018, and established lizard limb-length and density treatments at the end of the September 2018 fieldtrip. We exhaustively recaptured individually marked lizards and collected posttreatment food web data in May 2019. Our 8-mo experiment was sufficiently long to measure target ecological processes but short enough that mortality did not substantially alter relative treatment densities and evolution did not change trait values.

Results

We captured and measured 488 male brown anoles for our experiment, and we released a total of 220 of these lizards onto the 16 study islands (Fig. 1 *B* and *C* and *SI Appendix*, Fig. S1). Of the released lizards, 99.4% were inside the 30% long and short tails of the hindlimb length distribution, 97.7% were inside the 25% tails, and 93.2% were inside the 20% tails (Fig. 1*C*). At the median SVL of 47.5 mm, there was a 7.1% difference in hindlimb length between the long (36.43 mm) and short (33.86 mm) treatments (*SI Appendix*, Fig. S1; difference between treatments: $t_{64.2}$ = 4.58, P = 0.0001). Extreme long- and short-limbed individuals of similar SVL (54 mm) had a 6 mm or ~15% difference in hindlimb length (Fig. 1*B*). Relative hindlimb lengths in short- and long-limbed treatments closely corresponded to limb lengths observed in naturally occurring populations on small and large islands, respectively (Fig. 1*D*; island category effect: $F_{3,56.7}$ = 20.9, $P < 0.0001$); post-hoc Tukey's contrasts showed significant pairwise differences between all island categories except large islands—long-limbed treatment [P = 1.0]—and small islands—short-limbed treatment [P = 0.84].

Of the 220 lizards released in September 2018, we recaptured 62 in May 2019 and identified them based on their tags, finding only 6% tag loss for these lizards and no lizards missing both of their tags. There was a high correlation between the numbers of lizards released and recaptured among islands (r = 0.70, $P < 0.0001$), indicating that treatments maintained relative differences in density during the experiment. An additional five unique lizards were sighted, but not recaptured. Including these nonrecaptured lizards, the overall survival was 30.5% (67 of 220 lizards released) and ranged from 0 to 71% among the 16 experimental islands (*SI Appendix*, Table S1). For survival, there was no effect of density treatment (χ^2 = 0.07; df = 1; P = 0.33), limb-length treatment (χ^2 = 0.01; df = 1; P = 0.58), or their interaction (χ^2 = 1.23; df = 1; P = 0.26). Our exploratory analysis of associations between survival and other morphological traits found a marginally significant tendency for increased survival with increasing head width (χ^2 = 2.86; df = 1; P = 0.09), but not head length (χ^2 = 0.83; df = 1; P = 0.36). Body length and body mass were not associated with survival (P > 0.5 in both cases).

Table 1. Statistical results for the effects of brown anole limb length and density on lower trophic levels

Response variable	Effect	F	df	P
Web spider density	Pretreatment covariate	8.87	1,8.5	0.043^{*}
	Lizard density	0.18	1,8.2	0.68
	Lizard limb length	0.02	1,9.8	0.91
	Lizard density * limb length	8.73	1,8.2	0.018^{*}
Salticid spider density	Pretreatment covariate	0.28	1,10.2	0.61
	Lizard density	3.40	1,8.4	$0.10^{\dagger}$
	Lizard limb length	3.52	1,8.3	$0.096^{\dagger}$
	Lizard density * limb length	0.00	1,8.2	0.96
Buttonwood growth	Pretreatment covariate	0.30	1,28.8	0.59
	Lizard density	1.05	1,9.7	0.33
	Lizard limb length	3.37	1,9.1	$0.099^{\dagger}$
	Lizard density * limb length	8.90	1,9.1	0.015^{*}
Buttonwood leaf damage	Pretreatment covariate	4.20	1,23.8	$0.052^{\dagger}$
	Lizard density	0.06	1,11.5	0.82
	Lizard limb length	2.12	1,8.8	0.18
	Lizard density * limb length	1.12	1,9.5	0.32

See *Methods* for statistical model details and Fig. 2 for simple effects associated with the interactions between lizard density and limb length.
$^{*}P \leq 0.05$.
$^{\dagger}P \leq 0.10$

Lizard growth was greater in smaller individuals (F = 65.35; df = 1,57.9; $P < 0.01$), but did not differ between density treatments (F = 1.08; df = 1,25; P = 0.37) or limb-length treatments (F = 0.14; df = 1,11.9; P = 0.51); there was no significant interaction between lizard density and limb-length treatments for lizard growth (F = 0.09; df = 1,58; P = 0.77). Thus, our limb-length and density treatments had no effect on lizard growth or survival.

Effects of brown anole limb length on spiders and plants were largely consistent with predictions based on locomotor performance and foraging ability of lizards. For the density of web spiders, we found a significant interaction between limb-length and density treatments (Table 1; Fig. 2*A*). On islands with short-limbed lizards that we predicted would have stronger effects on arboreal prey, web spider density was reduced by 41% in the high-density treatment compared to the low-density treatment (t = 2.4; df = 8.25; P = 0.04), whereas on islands with long-limbed lizards, web spider density was not significantly different between the high- and low-density treatments (t = 1.8; df = 8.17; P = 0.11). For the density of salticid spiders, which are often ground dwelling, there was no interaction between limb-length and density treatments. However, salticid spider density was marginally reduced ($P \leq 0.10$) on islands with long-limbed lizards and on islands with high lizard density (Table 1 and Fig. 2*B*).

Buttonwood shoot growth revealed a significant interaction between lizard limb-length and density treatments (Table 1 and Fig. 2*C*). At high lizard densities, shoot growth was increased by 102% in the short-limbed treatment compared to the long-limbed

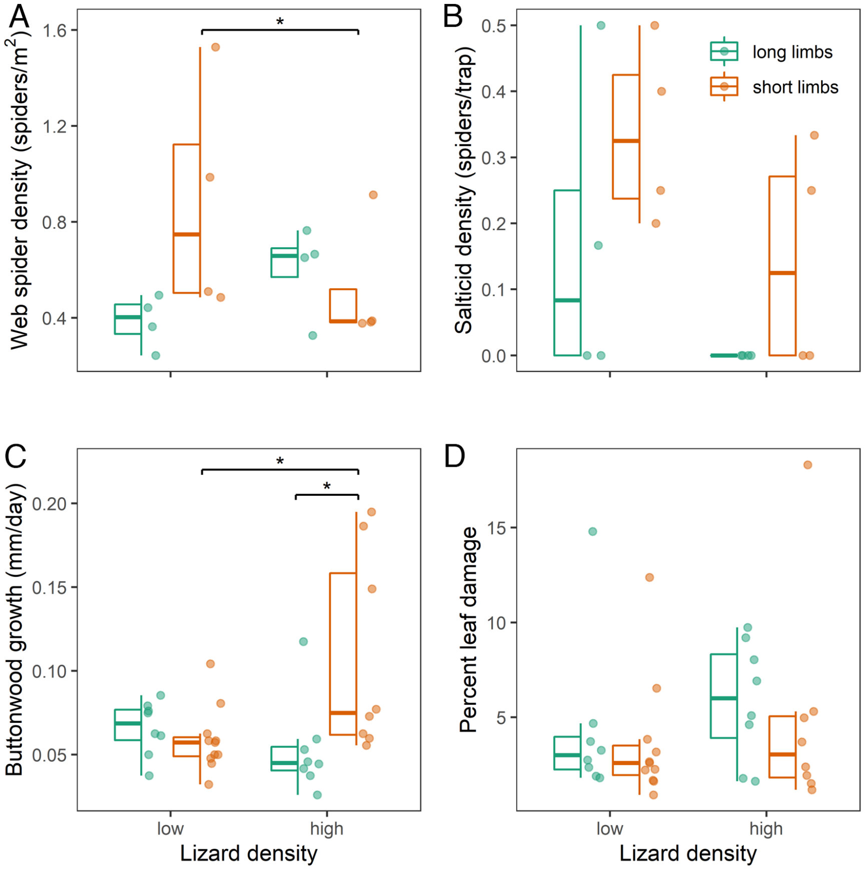

Fig. 2. The effects of brown anole limb length and density on spider abundance and plant growth. Panels show (*A*) web spider density, (*B*) salticid spider density, (*C*) buttonwood shoot growth, and (*D*) buttonwood leaf damage for the four types of experimental islands (i.e., long and short limbs crossed with low and high density). Points represent island-level measurements for spiders and plant-level measurements for shoot growth and leaf damage. Asterisks indicate statistically significant ($P < 0.05$) simple effects from post-hoc contrasts; for web spiders, there was a marginally significant difference ($P = 0.07$) between limb length treatments at low densities.

treatment (t = 3.4; df = 10.15; $P = 0.007$), whereas at low lizard densities, there was no significant difference in shoot growth between the short- and long-limbed treatments (t = 0.8; df = 8.08; $P = 0.44$). On islands with short-limbed lizards, shoot growth was increased by 81% in the high-density treatment compared to the low-density treatment (t = 2.8; df = 8.60; $P = 0.02$). There were no significant treatment effects on leaf damage (Table 1 and Fig. 2*D*).

Discussion

Consistent with our expectations, we found that short-limbed brown anoles had stronger cascading effects on plant growth than those of long-limbed lizards. Specifically, plants grew faster on islands with short-limbed lizards than on islands with long-limbed lizards, but only at higher lizard densities. A similar pattern was observed for web spiders: Higher densities of short-limbed lizards were associated with reduced web spider density. These results suggest that short-limbed brown anoles (which are expected to be better adapted for arboreal foraging on small islands than long-limbed brown anoles) can exert stronger direct top-down effects on prey and stronger indirect herbivore-mediated cascading effects on plants if the density of those lizard predators is relatively high. We found no effect of limb length on lizard survival or body condition and relative treatment densities remained similar despite mortality during the experiment, suggesting that the enhanced top-down effects of short-limbed lizards were driven primarily by increased efficacy of arboreal foraging rather than differential survival.

Our experimental results using realistic values for brown anole limb length and density based on long-term data provide unprecedented support for an evolution-to-ecology connection in nature. Short-limbed lizards at higher density have direct negative effects on prey and indirect positive effects on plants. We can infer an eco-evolutionary scenario in which strong food web effects are likely to occur based on our previous findings detailing how brown anole limb length and density change following island colonization (4, 26) along with the extensive variation in limb length among populations in the Bahamas (36). When propagules of brown anoles from larger islands were experimentally introduced to small islands, these populations increased in density and rapidly evolved shorter limbs in response to narrower vegetation (4, 26). In fact, the 7.1% difference in hindlimb length between treatments in our experiment closely mirrors the natural 6.5% decrease in hindlimb length of male lizards over the course of 3 y following experimental colonization (26). Both an increase in density and a reduction in limb length are expected to strengthen independently the top-down effects of brown anoles on the arboreal components of island food webs. However, our results suggest that concurrent change in traits and density may amplify top-down effects during the process of colonization, as changes in either density or limb length by themselves did not increase the effects brown anoles had on plant growth (Fig. 2*C*). In other words, enhanced top-down effects of predators during colonization may be the result of co-occurring ecological and evolutionary changes.

While our study documents an evolution-to-ecology connection by manipulating traits in a whole-island field experiment, previous laboratory and mesocosm experiments support similar connections for a variety of effects of intraspecific trait variation on ecological processes (e.g., refs. 14, 15, 19, and 39). For example, Ousterhout et al. (20) found a selection-driven trait-mediated indirect effect in which the cascading effects of natural selection imposed by fish favored less-active damselflies, leading to weaker predation effects on zooplankton, and ultimately a reduction in primary production. In contrast to our findings, this and other laboratory and mesocosm studies have tended to find more pronounced impacts of traits on top-down effects at low predator densities (18, 20). In some cases, this may be the result of resource depletion at high predator densities; for example, high densities of damselflies may consume enough zooplankton to mask the effects of trait differences (20). These issues are less likely to occur in our experiment, where predator densities remained well within the range of naturally occurring densities on small islands in the Bahamas, and prey resources can be replenished through dispersal. Although mesocosm experiments tend to show greater magnitudes of top-down effects than those of field experiments (40, but see ref. 41), the strong effects of brown anole limb length variation on prey density and plant growth in our experiment suggest that these previous evolution-to-ecology connections identified in laboratory and mesocosm experiments can be realized in nature.

Conclusions

Our research in this study system illustrates the reciprocal ecological and evolutionary connections needed to complete an eco-evolutionary feedback loop (Fig. 3). Studies of contemporary evolution have previously demonstrated the ecology-to-evolution connection with island vegetation mediating the evolution of limb length in brown anoles (4, 26). Our current experiment manipulated trait and density values of populations using hundreds of lizards and followed multilevel food web effects in replicate, whole-island ecosystems. Our experimental results provide clear evidence for an evolution-to-ecology connection—short-limbed lizards enhance plant growth—resulting in the potential for a positive eco-evolutionary feedback loop. The evolution of shorter limbs in brown anole populations enhances buttonwood growth, which should increase the ratio of narrow-to-broad diameter vegetation. In turn, the greater availability of narrow-diameter vegetation should select for brown anoles with shorter limbs (a narrow-sense eco-evolutionary feedback, 14). Other context-dependent feedback scenarios involving more than one phenotypic trait and ecological variable are also possible, especially those involving how top-down effects on food webs would be altered by the well-documented morphological and density changes associated with hurricanes (37, 42, 43) and the introduction of an intraguild predator (24, 25, 37). Given that empirical demonstrations of eco-evolutionary feedbacks are rare in nature (but see ref. 44), future research should focus on closing eco-evolutionary feedback loops. Our results validate evolution-to-ecology connections in nature, the importance of which will only increase as human activities continue to accelerate the pace of ecological and evolutionary change (45, 46).

Methods

Study System and Experimental Design. Our study was conducted on small islands near the much larger island of Great Abaco in the Bahamas. At the basal level, food webs on these islands are dominated by small trees and shrubs; one of the most common being buttonwood (*Conocarpus erectus*). Various arthropods fill most of the other trophic roles, while the predatory brown anole lizard (*A. sagrei*) is the most common, and often the only, terrestrial vertebrate.

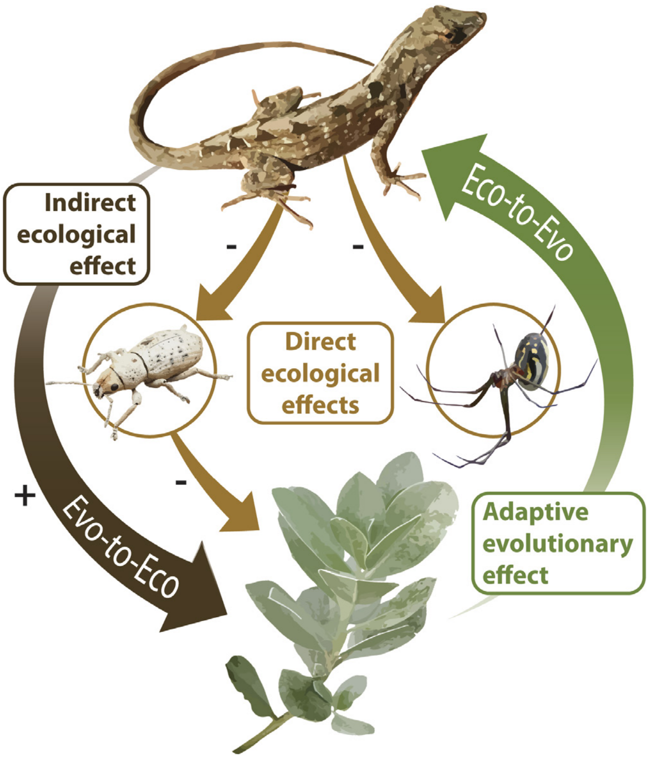

Fig. 3. Eco-evolutionary feedback loop for small-island ecosystems in the Bahamas. Our experiment showed that when narrow-diameter vegetation is common, short-limbed lizards directly reduce arboreal spiders (light brown arrow) and indirectly promote plant growth (dark brown arrow) through an herbivore-mediated trophic cascade (light brown arrows) (29–31, 35). These results provide crucial support for an evolution-to-ecology connection in nature (dark brown arrow labeled "Evo-to-Eco"). Based on our prior research (4, 24, 26), we contend that plant growth caused by this indirect positive effect of short-limbed lizards will increase the availability of narrow-diameter vegetation, which selects for short-limbed lizards that are more efficient arboreal predators. This adaptive evolutionary effect constitutes an ecology-to-evolution connection (green arrow labeled "Eco-to-Evo") that would close an eco-evolutionary feedback loop. Images represent the brown anole (*A. sagrei*), multiple species of herbivores, multiple species of spiders, and buttonwood (*Conocarpus erectus*). Original photographs altered for publication under CC BY-NC 4.0 and CCO 1.0: brown anole (B. J. Stacey) and spider (D. J. Ringer).

Our experimental design featured factorial manipulations of brown anole limb length and density on 16 small islands ranging from 35 to 312 m^2 in vegetated area (*SI Appendix*, Table S1). The 16 islands were broken up into four blocks based on vegetated area, and the four treatments were assigned randomly to islands within each block. We collected pretreatment baseline data in May and September 2018. Brown anole introductions took place after baseline data collection in September 2018. Posttreatment data were collected in May 2019. To ensure that reproduction did not alter treatment densities and within-island limb length values, we only introduced adult male lizards to experimental islands.

To determine the appropriate high- and low-density treatments, we used all available population-size estimates from our long-term studies on nearby small islands occupied by brown anoles from 2008 to 2016 (N = 24 islands in total, with 12 of these islands having complete data for that time period). We calculated the maximum and minimum densities on each island from annual surveys during that time period and took the mean across all islands (mean maximum: 0.32 lizards/m^2; mean minimum: 0.07 lizards/m^2). Because we only introduced male lizards, we matched our high- and low-density treatments to the expected density of males on islands with mean maximum and mean minimum brown anole density (assuming a 1:1 sex ratio). In other words, our high-density treatment featured roughly 0.16 lizards/m^2 and our low-density treatment featured roughly 0.035 lizards/m^2 with some variation around these target densities as only integer values of lizards can be introduced to islands.

We implemented the long- and short-limbed treatments by capturing 488 adult male lizards from multiple localities on the island of Great Abaco

(*SI Appendix*, Table S2), measuring their body size (i.e., SVL) and hindlimb length, and using 220 individuals that represented the tails of the distribution of relative hindlimb length (calculated as the residuals of the regression of ln[hindlimb length] on ln[SVL]) in our experiment, Fig. 1*C*). We do not expect substantial changes in relative limb length due to phenotypic plasticity over the course of the experiment, due to the relatively short duration of the experiment (i.e., 8 mo) and the use of only adult lizards, which grow much slower than hatchlings and juveniles.

To put our long- and short-limb treatments in the context of limb length variation found on large and small islands throughout the Bahamas, we compared relative hindlimb length for the 220 male brown anoles introduced to islands in our experiment to 912 male brown anoles from populations on 13 large and 35 small islands. The data from these naturally occurring populations were collected over a 17-y period (1992 to 2009) from large islands throughout the Bahamas (36), small islands near Staniel Cay in the Exumas (4), and our Snake Cay study area in Abaco (26).

Data Collection for the Limb Length– –Density Experiment. Brown anoles introduced to experimental islands in September 2018 were individually tagged using two 3-mm tags with unique alphanumeric codes (Northwest Marine Technology, Inc.). We subcutaneously injected tags on the ventral side of each hindlimb such that tags could be read through the skin with the aid of an ultraviolet light. Previous studies have shown that some tag loss occurs in brown anoles and inserting two tags allowed us to identify individual lizards even if one tag was lost (25). We exhaustively recaptured remaining individuals in May 2019 to estimate individual and population-level survival and measured SVL to calculate individual growth in body size over the 8-mo experimental period. We visited each island three to six times with one to three observers for a total of 193 to 704 min per island, with our effort being proportional to the number of lizards released on each island ($r = 0.79$, $P < 0.0001$).

We collected data on spider abundance, plant growth, and leaf damage following established methods (31, 47). Web spider censuses were conducted by counting each web spider or intact web on each study island; we then calculated web spider density by dividing the total by island vegetated area. We measured salticid spider density using bowl traps consisting of a plastic bowl with water and a small amount of detergent left out for 24 h; each island had between two and six bowl traps, with the number of traps scaled to island vegetated area. At the end of the sampling period, the bowls were collected, and salticid spider density was calculated as the number of spiders per trap. Plant growth and leaf damage data were collected from buttonwood plants on each experimental island. Prior to the assignment of treatments, we selected two to three buttonwood plants per island. Shoot growth was measured by marking the most apical leaves on four stems per plant at the beginning of a sampling period and measuring shoot elongation at the end of each sampling period as the distance from the most apical marked leaf to the end of the shoot. These shoot elongation measurements were divided by the number of days in the sampling period to generate measurements of daily growth rates. Leaf damage was measured by haphazardly collecting 10 leaves from each study plant and analyzing the images using ImageJ (48) to quantify the proportion of leaf area that was damaged. These data were collected in September 2018 (pretreatment) and May 2019 (posttreatment).

Statistical Analysis. We used linear mixed models to confirm that our long- and short-limbed treatments differed in limb length and to compare lizard relative limb length on islands in our experiment with those in naturally occurring lizard populations on large and small islands. The response variable was ln[hindlimb length] for each individual lizard measured; ln(SVL) was used as a continuous covariate so that any differences between groups represent differences in relative hind limb length. Island category (short-limbed treatment, long-limbed treatment, large island, small island) was a fixed effect and island was a random effect.

We evaluated the interactive effects of lizard density and limb length on web spider and salticid spider density using linear mixed models. Spider density was the response variable with separate models to evaluate arboreal web spiders and salticid spiders (the latter being more ground dwelling). We log-transformed densities prior to analysis to meet assumptions of homoscedasticity and normality of residuals. Since the density of salticid spiders was zero for some islands, we added 0.1 (approximately equal to the minimum nonzero measurement) to all raw salticid spider densities to avoid taking the log of zero. The fixed effects were limb length (short vs. long), density (high vs. low), and their interaction; mean spider density from the two pretreatment samples was used as a continuous covariate; experimental block was included as a random effect. Models of buttonwood shoot growth and leaf damage were like those for spiders, but the response variables (i.e., daily growth rate and percent leaf damage) were measured for each individual study plant, so the models also included a random effect of island to account for the nonindependence of plants from the same island. The models for web spider density and buttonwood growth generated a singular fit, likely because the variance estimate for the block random effect was zero. Removing block from the analysis generated qualitatively similar results; we present results from the model with block included.

We tested for treatment effects on lizard survival using a generalized linear mixed model with a logit link function and a binomial error distribution (i.e., a mixed logistic regression). Individual lizards recaptured in May 2019 survived, while those not recaptured in May 2019 were assumed to have not survived. Density and limb length treatments, as well as their interaction, were included as fixed effects and the identity of the experimental island was included as a random effect. Because survival may be associated with other morphological traits (in addition to relative hindlimb length), we also explored relationships between survival and body size (SVL and mass) and relative head length and width. These four variables were included as a continuous covariate in separate mixed logistic regressions of survival that also included island identity as a random effect. Relative head dimensions were calculated as the residuals of the regression of ln-head length or width on ln-SVL. This was intended to be an exploratory analysis rather than a confirmatory analysis, so the results are interpreted with caution. Additionally, we used linear mixed models to evaluate treatment effects on lizard growth, which was measured as the difference between initial SVL at the time of translocation and SVL at the time surviving lizards were recaptured 8 mo later. Lizard growth was square root transformed prior to analysis to meet assumptions of homoscedasticity and normality of residuals. We tested whether lizard growth was associated with density and limb length treatments as well as the interaction, including initial SVL as a covariate because growth rate declines as lizards increase in size (49, 50).

All analyses were conducted using R (51); linear mixed models and generalized linear mixed models were fit using functions in the "lme4" package (52). Hypothesis tests for linear mixed models were conducted using *F*-tests, with denominator degrees of freedom calculated using the Kenward–Roger method. Post-hoc *t* tests used a similar approach and were performed using the "lmerTest" (53) and "emmeans" packages (54). Hypothesis tests for generalized linear mixed models were conducted using likelihood ratio tests.

Data, Materials, and Software Availability. Data reported in this paper are deposited in the Dryad digital repository (https://doi.org/10.5061/dryad.70rxwdc3p) (55) All study data are included in the article and/or *SI Appendix*.

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