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Recolonization of secondary forests by a locally extinct Caribbean anole through the lens of range expansion theory

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Abstract

Disturbance and recovery dynamics are characteristic features of many ecosystems. Disturbance dynamics are widely studied in ecology and conservation biology. Still, we know less about the ecological processes that drive ecosystem recovery. The ecological processes that mediate ecosystem recovery stand at the intersection of many theoretical frameworks. Range expansion theory is one of these complementary frameworks that can provide unique insights into the population-level processes that mediate ecosystem recovery, particularly fauna recolonization. Although the biodiversity patterns that follow the fauna recolonization of recovering forests have been well described in the literature, the ecological processes at the population level that drive these patterns remain conspicuously unknown. In this study, we tested three fundamental predictions of range expansion theory during the recolonization of recovering forests in Puerto Rico by a shade specialist anole, *Anolis gundlachi*. Range expansion theory predicts that individuals at the early stages of recolonization (i.e., younger forests) would have a high prevalence of dispersive traits, experience less density dependence, and suffer less parasitism. To test these predictions, we conducted a chronosequence study applying space-for-time substitution where we compared phenotypic traits (i.e., body size, body condition, and relative limb size), population density, population growth rates, and *Plasmodium* parasitism rates among lizard populations living in young (<30 years), mid (~40–70 years), and old-growth forests (>75 years). Lizard populations in younger forests had lower densities, higher population growth rates, and lower rates of *Plasmodium* parasitism compared with old-growth forests. Still, while we found that individuals had larger body sizes, and longer forelimbs in young forests in one site, this result was not consistent among sites. This suggests a potential trade-off between the traits that provide a dispersal advantage during the initial stages of recolonization and those that are advantageous to establish in novel environmental conditions. Overall, our study emphasizes the suitability of range expansion theory to describe fauna recolonization but also highlights that the ecological processes that drive recolonization are time-dependent, complex, and nuanced.

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INTRODUCTION

Disturbance and recovery dynamics are characteristic features of many ecosystems (Johnstone et al., 2016; Turner, 2010; White & Jentsch, 2001). In some cases, the disturbance has natural causes like hurricanes (Lugo, 2008), fire (McLauchlan et al., 2020), or other consequences of climate change (Seidl et al., 2017). In others, disturbance is more directly linked to human activities such as land-use change (Song et al., 2018). Regardless of the source, disturbance, and recovery dynamics are central to our understanding of the Anthropocene landscape (Newman, 2019; Rozendaal et al., 2019).

The ecological processes that mediate ecosystem recovery stand at the intersection of many theoretical frameworks (Poorter et al., 2021, 2023). Range expansion theory is one of these complementary frameworks that can provide unique insights into the ecological processes that govern ecosystem recovery. While range expansion is commonly applied to study ecological invasions (e.g., Hastings et al., 2005), this framework is generally applicable to any type of expansion in which a population expands into a site where it is currently absent (Eigentler et al., 2022). For instance, range expansion theory informs our understanding of climate-related shifts (Lenoir & Svenning, 2015), disease spread (Rees et al., 2009), and native species expansions (Diggins, 2023). Recently, range expansion theory has been proposed as a useful framework to understand the population-level processes that drive fauna recolonization during ecosystem recovery (Acevedo et al., 2023). Based on the fundamental assumption that recolonizing populations are composed of a small nonrandom subset from a source population, range expansion theory predicts that recolonizing populations (1) will be composed of individuals with phenotypic traits that reflect a greater ability for dispersal, (2) will experience higher population growth rates due to less density regulation, and (3) will experience escape and release from co-evolved natural enemies. Supporting evidence for these predictions is common in other types of expansions (Chuang & Peterson, 2016), yet it is unknown if these hypotheses would be supported during fauna recolonization.

Range expansion theory predicts that individuals with long-distance dispersive traits, including longer limbs, larger body sizes, or better body condition would be more represented in the expansion front (Phillips et al., 2010). Longer limbs or larger bodies are traits that can help

individuals move more effectively through difficult landscapes. Also, individuals with larger body sizes or better body condition may store more fat reserves, which may be beneficial when dispersing long distances through a hostile matrix with limited access to food resources. There are multiple empirical examples of this pattern. For example, cane toads in Australia with longer limbs, bush crickets with longer wings, and silver-spotted skipper butterflies with longer wings are overrepresented in their expansion fronts (Braschler & Hill, 2007; Phillips et al., 2007; Simmons & Thomas, 2004). Also, coyotes expanding their range northward and eastward in North America (Thurber & Peterson, 1991) and damselflies expanding their range at higher latitudes in Europe have larger body sizes (Hassall et al., 2014). This overrepresentation of dispersive traits at the edge of the expansion front is also known as spatial sorting and is characteristic of pulled expansions. In this type of expansion, the dynamics at the edge of the front are the ones "pulling" the population spread (Gandhi et al., 2016). Alternatively, recolonizing populations may be the result of pushed expansions where, instead of a continuous wave with highly dispersive individuals at the edge of the expansion front, individuals may recolonize from nearby sources at carrying capacity. In this type of expansion, the individuals that venture out looking for alternative habitats may not necessarily be dispersive and dominant individuals but subordinate ones escaping density dependence. This pattern has been observed in the territorial lizard *Anolis sagrei* where smaller-sized individuals are overrepresented in the founding population because competitive interactions in the core population drive smaller-sized individuals to disperse away (Calsbeek, 2009). Last, there could be trade-offs between the phenotypic traits that give a dispersal advantage and those optimal to successfully establish populations in recovering habitats. For instance, longer limbs may give a dispersal advantage to animals during transit from old-growth to recovering forests. However, recovering forests often have open canopies, complex understories, and smaller trees (Rios-López & Mitchell Aide, 2007), for which having smaller bodies and limbs would be more advantageous. If this trade-off between dispersive traits and those that are adaptive to the recolonizing habitats is strong, observed phenotypic patterns in recolonizing populations would likely depend on the time since initial colonization. As time since initial colonization increases, we would expect

dispersive traits to become less prevalent in the population as they are being replaced by traits that may be more advantageous in novel environmental conditions.

Individuals in the expansion front are predicted to experience r-selected environments (Burton et al., 2010; Phillips et al., 2010), resulting from a decrease in density dependence or a shift in life-history strategies such as larger clutch sizes, early breeding season, or increased breeding rates of smaller females. For instance, invasive cane toads in Australia and expanding populations of mountain goats in Greater Yellowstone have higher population growth rates than their core populations (Flesch et al., 2016; Phillips, 2009). Also, high population growth rates in the European bat species *Rhinolophus hipposideros* are driven by higher rates of juvenile survival that ultimately lead to higher net reproductive output (Jan et al., 2019). A pattern of high population growth rates from colonizing at low densities can result from pulled expansions that assume a small role of Allee effects. Alternatively, in push expansion density dependence in the source populations would push individuals to the edges and beyond potentially resulting in a continuous influx of recolonizing individuals that maintain a minimum viable population size and genetic diversity. This influx would increase through time, as recovering sites mature and continue to develop conditions that are favorable for recolonization and establishment. As time progresses recovering sites would reach equilibrium and conditions would resemble k-selected environments.

Recolonizing populations are predicted to experience escape and release from parasitism. The small recolonizing population is expected to include a proportionally small number of infected individuals (Phillips et al., 2010). This enemy release hypothesis has empirical support in a variety of expanding populations. For example, the Brown Argus butterfly suffers less parasitoid mortality in newly colonized sites in Britain than in long-established populations (Menéndez et al., 2008). Similarly, invading populations of cane toads in tropical Australia are virtually lungworm-free during their expanding phase (Phillips et al., 2010). Experimentally, the gall-forming insect *Neuroterus saltatorius* (Insecta: Hymenoptera: Cynipidae) suffers fewer parasitoid attacks on the invasion front (Prior & Hellmann, 2013). The low rates of parasitism would free up resources that individuals can allocate toward reproduction leading to higher population growth rates particularly when combined with low-density regulation (see below; Perkins et al., 2008). Demographic and environmental stochasticity may continue to keep the rates of parasitism low at the early stages of recolonization. However, as time progresses the rates of parasitism are expected to increase due to the continued immigration of individuals from the source population (Chan et al., 2015).

Recovering forests are becoming increasingly common, particularly in the tropics, where socioeconomic changes are driving the abandonment of agricultural areas (Aide & Grau, 2004; Grau et al., 2003). These abandoned areas undergo succession and in 20–40 years they can develop complex forest structures that allow for the recolonization of most animal species (Acevedo-Charry & Aide, 2019). While animal biodiversity patterns in recovering forests have been well described in the literature, we know little about the ecological processes at the population level that ultimately drive these patterns. Long-term studies that follow populations through time are the gold standard for better understanding fauna recolonization. Yet, these long-term studies are expensive, logistically challenging, and often unfeasible (Franklin, 1989; Lindenmayer et al., 2012). Alternatively, chronosequence studies using space-for-time substitutions have been used successfully to study animal recolonizations (e.g., Acevedo-Charry & Aide, 2019; Hilje & Aide, 2012). Here, we tested three fundamental predictions of range expansion theory (e.g., high prevalence of dispersive traits, less density dependence, and escape and release of parasites) in the recolonization of recovering forests by the shade specialist anole (*Anolis gundlachi*) in chronosequences including young (<30 years), mid (~40–70 years), and old-growth (>75 years) forests in Puerto Rico. Support for range expansion predictions would include a higher prevalence of lizards with larger bodies, longer limbs (relative to body size), and/or better body condition in young forests compared with older forests. Similarly, we would expect lower densities, higher population growth rates, and lower parasitism rates in the younger forests compared with older ones.

METHODS

Study system

We conducted the study in Puerto Rico, a Caribbean island that underwent a dramatic increase in forest cover going from less than 10% at the beginning of the 20th century to more than 50% today (Martinuzzi et al., 2022). This forest cover increase was the result of socioeconomic changes in the 1950s that incentivized manufacturing leading to rural–urban migration and the abandonment of agricultural areas (Grau et al., 2003). These abandoned areas recovered and today Puerto Rico is a land-cover mosaic composed of forests of different ages, agricultural, and urban areas (Kennaway & Helmer, 2007). This

makes it an ideal setting to understand the ecological consequences of forest recovery and fauna recolonization.

Chronosequence studies using space-for-time substitutions are common in the study of fauna recolonization (synthesized by Acevedo-Charry & Aide, 2019). We assessed forest age using a combination of published land-cover maps (Kennaway & Helmer, 2007), inspection of aerial photographs in Google Earth, and confirmation with physical visits to the sites, and conversations with residents. We initially evaluated more than 15 potential chronosequences in Puerto Rico. Out of these, three met our selection criteria (Appendix S1: Figure S1). These criteria included that (1) young (<30 years), mid (~40–70 years), and old-growth forest (>75 years) coexisted within 2.5 km of each other to control for local factors, (2) they are in mid-low elevation (<500 m) to control for forest type, (3) the study species, *A. gundlachi*, is present in all three forest ages, and (4) the sites are accessible and safe for researchers to sample. The three chronosequences ultimately selected were in the Luquillo (EV) and the Cayey (Carite1 and Carite2) municipalities (Appendix S1: Figure S1). The forest types included subtropical wet or tropical montane forests depending on the life zone classification system used (Ewel & Whitmore, 1973; Walsh, 1996).

Our study species, *A. gundlachi*, is a medium-sized anole (mean snout-to-vent length of 48.76 mm and mean mass of 3.56 g) belonging to the trunk-ground ectomorph often reaching abundances of 2000 ha^{-1} (Reagan, 1992). It is the most common anole in the understory of this type of forest. This species is a thermoconformer-shaded forest specialist whose metabolism is closely linked to environmental temperature (Huey & Webster, 1976). Therefore, the distribution of this species is linked to a layered closed canopy typical of more mature forests. This anole species will recolonize younger secondary forests only if they are structurally well-developed. This makes it an appropriate species to study fauna recolonization. This anole species is parasitized by three *Plasmodium* species: *P. azurophilum*, *P. floridense*, and *P. leucocytica*. The first two infect red blood cells while the latter infects white blood cells. The overall prevalence varies by year and fluctuates between 10% and 40%. Out of the three, *P. azurophillum* is the most common accounting for more than 60% of the infections (Otero et al., 2019). These are vector-borne parasites, and their vector in Puerto Rico is hypothesized to be a widely distributed *Culex* mosquito species (Reeves et al. unpublished).

Experimental design

We sampled Carite1 in June 2019, Carite2 in June and December 2021, and El Verde in December 2018,

May and December 2019, June and December 2021, and June 2022. We incorporated sampling season as a random effect in the analyses whenever it was appropriate (see below). To quantify phenotypic traits, we captured animals inside 20×20 m plots at each forest age (i.e., young, mid, old). Within these forest ages we aimed to maximize the number of individuals sampled while ensuring the safety of the researchers. In Carite1 we sampled one plot per forest age, in Carite2 two plots in old forest, one in mid forest, and one in the young forest. In El Verde we sampled four plots in old forest, four plots in mid forest, and two plots in young forests. The uneven number of plots sampled per site responds to variations in forest patch size and accessibility. To maximize our sample size in El Verde, we also included in the analyses of phenotypic traits 142 individuals captured near but outside the plots (within the same forest patch). Plots were separated by >50 m, which is an appropriate distance to ensure independence among plots because, even though lizards move through the forest, *A. gundlachi* is highly territorial, and it is not uncommon to recapture the same individual in the same tree. After capture, individuals were kept in individual cloth bags and brought to a measuring station. At this station, we sexed the individuals and assessed their overall health condition. Weak animals were returned immediately to the forest. If healthy, we measure snout-to-vent length (SVL) using a clear ruler, weight using a 10 g Pesola, and limb sizes (right front and back limbs) using an analog caliper. Within a sampling season, the same researcher made all limb measurements which minimized any potential observer bias in the measurements. We marked individuals with a beetag and/or visual-implanted elastomer to prevent sampling an individual more than once. After taking these measures and samples the individuals were returned to the sites where they were captured within 24 h.

To estimate abundance by forest age we conducted distance sampling in El Verde and Carite2. We established a 50 m transect in each forest age patch in Carite2. In El Verde we established four transects (of the same length, 50 m) in old forest and mid forest, and two transects in the young forest. A trained observer walked the 50 m transects and noted the distance and angle to every individual detected. The same observer surveyed the three forest ages to limit potential observer bias. The distance to the observer was quantified using a Bosch Blaze laser distance measurer and the angle from the main heading using a compass. We used these distances and angles to calculate perpendicular distances to the transect using trigonometric functions (see below). We conducted distance sampling at El Verde in May 2019 and June 2021 to estimate the population growth rate.

These surveys were conducted in the summer to control for any potential seasonal variation.

To assess infection status, we analyzed data from El Verde in May 2019 and from Carite1 (June 2019) and Carite2 (June and December 2021). We sample adult males and females (SVL > 40 mm) due to the difficulty of safely sampling blood from small individuals. We performed a tail tip clip to collect a blood sample (1–2 drops) in cellulose paper for molecular diagnostics. We extracted DNA from these samples using the DNeasy Blood & Tissue Kit (Qiagen) and conducted a nested PCR to amplify potential parasite sequences present in the blood samples. We used primers specific for lizard *Plasmodium* (Perkins & Schall, 2002, see also Appendix S1) but currently there are no malaria species-specific primers available. After the nested PCR procedure positive samples were detected in an electrophoresis gel with a band at ~500 bp and negatives when no band was found.

Analyses

To test for differences in body size (SVL) and weight among forest ages we modeled the log(SVL) and log(weight) in separate linear models as a function of sex and an interaction of forest age (young, mid, and old) and site (El Verde, Carite1, and Carite2). We used the log transformation to ensure the parametric assumptions of the model. To test for differences in male body condition we first calculated a residual body condition index (BCI). In this type of BCI each individual body condition is characterized as the residual of the linear relationship between $\log_{10}(\text{weight})$ as a function of $\log_{10}(\text{SVL})$. Then we used a linear model to predict these residuals as a function of an interactive effect of forest age and site. We conducted this assessment only on males because the presence of eggs in some females may bias their estimates of body condition. To test for differences in the relative size of limbs we conducted a linear model of the log of limb size (radius/ulna, humerus, femur, and fibula/tibia) as a function of log(SVL), sex, and an interactive effect of forest age and site. This type of analysis is commonly applied in studies of anoles that aim to compare the size of limbs relative to body size (e.g., Acevedo et al., 2022; Donihue et al., 2018). In these models we used the category "old forest" as the baseline for forest age. We also used a likelihood ratio test to assess the need to add the season in which the data were collected as a random effect (Crainiceanu & Ruppert, 2004). If a mixed-effects model was appropriate, we made inferences using the Kenward and Roger likelihood ratio test (i.e., we reported F_{KR} and their corresponding p-values) comparing a model with and without forest age as a covariate and interpreting parameter estimates and their uncertainty (Kenward & Roger, 1997). To conduct these likelihood ratio tests we used the libraries RLRsim and pbkrtest in R (Halekoh & Højsgaard, 2014; R Core Team, 2023; Scheipl et al., 2008). If there was not enough evidence to justify a mixed-effects model, we made inferences on the corresponding fixed-effects model by interpreting beta coefficients and their corresponding t-test and p-values. We evaluated the overall model fit using the R^2 statistic.

To estimate abundances by forest age we fitted a half-normal detection function to the perpendicular distances calculated through transects (see above). To fit this model, we used the package Distance in R (Miller et al., 2019). We estimated the population growth rate as $\lambda = \frac{N_{t+1}}{N_t}$, where N_{t+1} represents abundance estimation in El Verde in the summer of 2021 and N_t represents abundance estimation in the summer of 2019. To estimate uncertainty around this estimate we estimated it iteratively after systematically removing one observation from each year's dataset for all combinations of observations removed.

Finally, to compare the probability of infection among forest ages we modeled the presence or absence of *Plasmodium* sp. parasites using a generalized linear model (GLM) as a function of forest age using a binomial distribution and a logit link function. Note that we also added sex as a controlling covariate because previous research shows that males have a higher probability of infection than females (Otero et al., 2019). We evaluated the overall model fit of this GLM using the McFadden R^2 statistic.

RESULTS

Phenotypic traits

To test for potential differences in phenotypic traits among forest ages we analyzed a total of $N = 766$ individuals from three sites: El Verde (EV), Carite1 (C1), and Carite2 (C2). At El Verde, we analyzed $N_{EV} = 648$ individuals, in Carite1 $N_{C1} = 33$, and in Carite2 $N_{C2} = 85$ (Appendix S1: Table S1).

We found support for the prediction of differences in body size among forest ages, but the direction of these differences varied by site. In El Verde, individuals living in the young forest were larger than those living in the old forest ($\beta_{EV,y} = 0.04 \pm 0.02$ SE, $p = 0.012$; Figure 1a). However, in Carite1 the pattern was reversed; individuals were significantly smaller in the young forest in comparison with the old forest ($\beta_{C1,y} = -0.13 \pm 0.06$ SE, $p = 0.026$). We found no clear statistical difference
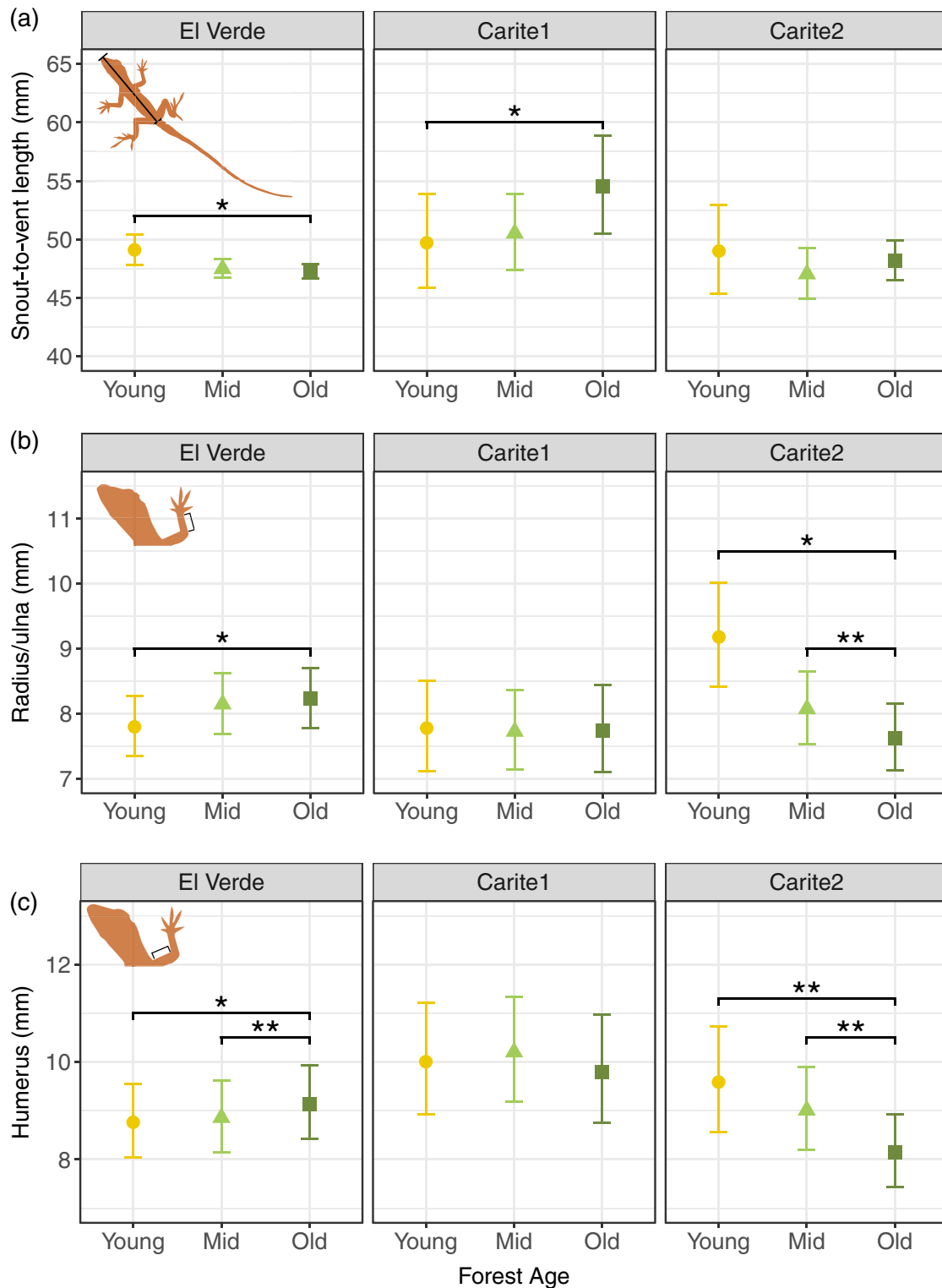
FIGURE 1 The figure shows model predictions for (a) snout-to-vent length (SVL), (b) relative size of the radius/ulna, and (c) relative size of the humerus of *Anolis gundlachi* among forests of different ages in three sites (El Verde, Carite1, and Carite2) in Puerto Rico. The large symbols and error bars represent mean and 95% confidence intervals (CI). Brackets emphasize clear statistical differences among forest ages (one asterisk represents $p < 0.05$, while two asterisks represent $p < 0.01$). For simplicity, the figure shows average predictions among males, females, and juveniles. Overall, these analyses show differences in phenotypic traits among forest ages where the direction varies by site. Silhouettes modified from PhyloPic.org under Creative Common license CC0 1.0.

between the size of individuals living in the young and old forest in the Carite2 site ($\beta_{C2,y} = -0.02 \pm 0.05$ SE, $p = 0.636$). We also found no clear differences between the size of individuals in the mid and old forests in any of the sites (Appendix S1: Table S2). Generally, individuals in Carite1 were larger than those in El Verde ($\beta_{EV,y} = 0.14 \pm 0.02$ SE, $p = 0.012$; Figure 1a). We made inferences on the fixed-effects model (i.e., no random effect of season) because the mixed-effects model had a singular fit. This fixed-effects model had an appropriate fit to the data ($R^2 = 0.65$). We found no clear statistical differences in weights among forests of different ages in either of the sites (Appendix S1: Table S3). We also found no clear statistical difference in males' body condition among forests of different ages ($F_{KR} = 1.91$, $p = 0.08$; Appendix S1: Table S4).

Similar to body size, we also found support for the prediction of differences in relative limb sizes among forest ages. We found clear statistical differences in the size of the radius/ulna relative to SVL ($F_{KR} = 5.62$, $p < 0.001$; Figure 1b), but these varied by site. In El Verde, the relative size of radius/ulna was smaller in the young forest when compared with the old-growth forest ($\beta_{EV,y} = -0.05 \pm 0.01$ SE). However, we found the opposite pattern in Carite2 ($\beta_{C2,y} = 0.24 \pm 0.04$ SE). Also, in Carite2 individuals in the mid forest had larger radius/ulna compared with the old-growth forest ($\beta_{C2,m} = 0.07 \pm 0.03$ SE). There was no clear statistical difference in the relative radius/ulna size between the young and old-growth forest in Carite1 ($\beta_{C1,y} = 0.06 \pm 0.05$ SE; Appendix S1: Table S5). We found no clear statistical differences in the relative sizes of radius/ulna of individuals living in the mid and old-growth forests in El Verde or Carite1 (Appendix S1: Table S5). We made inferences on a model that included sampling season as a random effect (LRT = 102.15, $p < 0.001$). This model had an appropriate fit to the data ($R_c^2 = 0.80$).

We also found clear statistical evidence of differences in the size of the humerus relative to SVL ($F_{KR} = 4.41$, $p < 0.001$; Figure 1c), but their magnitude and direction also varied by site. In El Verde, the relative size of the humerus was smaller in the young ($\beta_{EV,y} = -0.04 \pm 0.02$ SE) and mid ($\beta_{EV,m} = -0.03 \pm 0.01$ SE) forests when compared with the old-growth forest. We found the opposite pattern in Carite2 where individuals had larger relative humerus in the young ($\beta_{C2,y} = 0.21 \pm 0.05$ SE) and mid ($\beta_{C2,m} = 0.13 \pm 0.04$ SE) forests when compared with the old-growth forest. We found no clear evidence of differences in the relative size of the humerus among forest ages in the Carite1 site (Appendix S1: Table S6). We made these inferences on a model that included sampling season as a random effect (LRT = 304.32, $p < 0.001$). This model had an appropriate fit to the data ($R_c^2 = 0.77$). We

found no clear statistical evidence of changes in the size of the tibia/fibula ($F_{KR} = 1.21$, $p = 0.299$; Appendix S1: Table S7) or in the size of the femur ($F_{KR} = 1.91$, $P = 0.076$; Appendix S1: Table S8) relative to SVL.

Abundance and population dynamics

We found support for the prediction of lower population densities in the early stages of recolonization. The estimated mean abundance was lower in the young forests when compared with old forests and this effect was consistent in El Verde $\widehat{N}_{young} = 135.52 \pm 11.86$ SE; $\widehat{N}_{old} = 196.51 \pm 15.86$ SE; Figure 2 and Carite2 ($\widehat{N}_{young} = 111.36 \pm 18.23$ SE; $\widehat{N}_{old} = 190.9 \pm 28.99$ SE). There was no clear difference in abundance between mid and old forests (Figure 2). We also found support for higher population growth rates in young forests. The estimated population growth rate at El Verde was higher in the young forest ($\lambda_{young} = 3.06 \pm 0.001$ SE), followed by the mid ($\lambda_{mid} = 1.81 \pm 0.001$ SE), and old forests ($\lambda_{old} = 1.31 \pm 0.001$ SE).

Parasitism

To test for potential differences in parasitism rates among forest ages we analyzed a total of $N = 177$ individuals from three sites. At El Verde, we analyzed $N_{EV} = 87$ individuals, in Carite1 $N_{C1} = 27$, and in Carite2 $N_{C2} = 63$. We found support for the prediction of lower parasitism rates in the early stages of recolonization. The probability of malaria infection in the young forest was lower than in the old forest (Figure 3). The odds of infection in the young forest were 0.12 ± 0.08 SE times those of the old forest ($z = -2.14$, $p = 0.001$). We found no clear statistical difference in the probability of infection between mid and old-growth forest ($z = -0.46$, $p = 0.37$; Appendix S1: Table S9). The model predicts no clear difference between infection rates in Carite1 ($z = 0.32$, $p = 0.54$) or Carite2 ($z = 0.42$, $p = 0.26$) and El Verde site. Note that this model included and additive but not an interaction effect between site and forest age because we found no infections in the young forest in Carite1. This model had a moderate fit to the data ($R_{MF}^2 = 0.08$).

DISCUSSION

In this study, we tested three fundamental predictions of range expansion theory during the recolonization of recovering forests of a shade specialist anole in Puerto Rico. Following these predictions, we would expect a
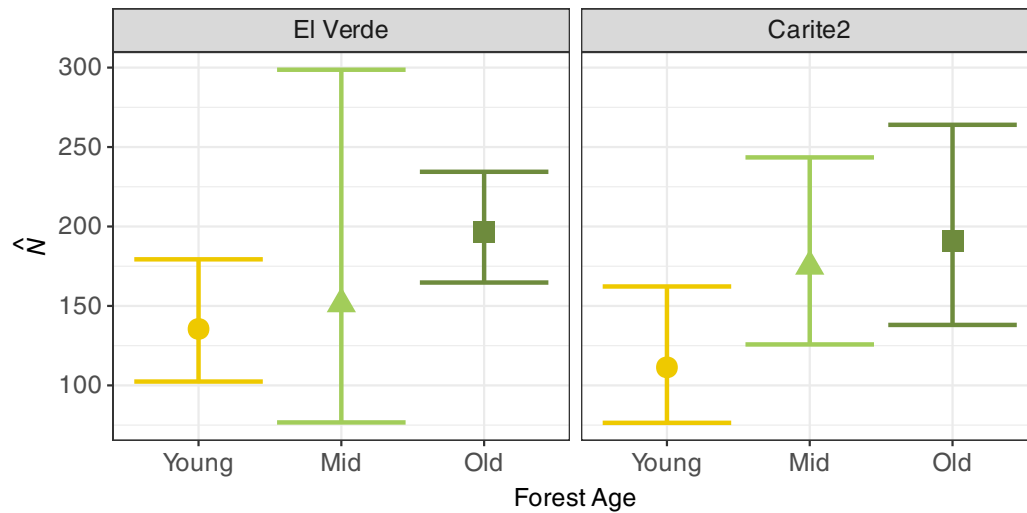
FIGURE 2 The figure shows abundance estimates from distance sampling by forest age in El Verde and Carite2. Both surveys were conducted in 2021. The models predict a lower abundance of individuals in the young forests compared with old-growth forest and this effect is consistent among sites. The large symbols and error bars represent mean and 95% CI.
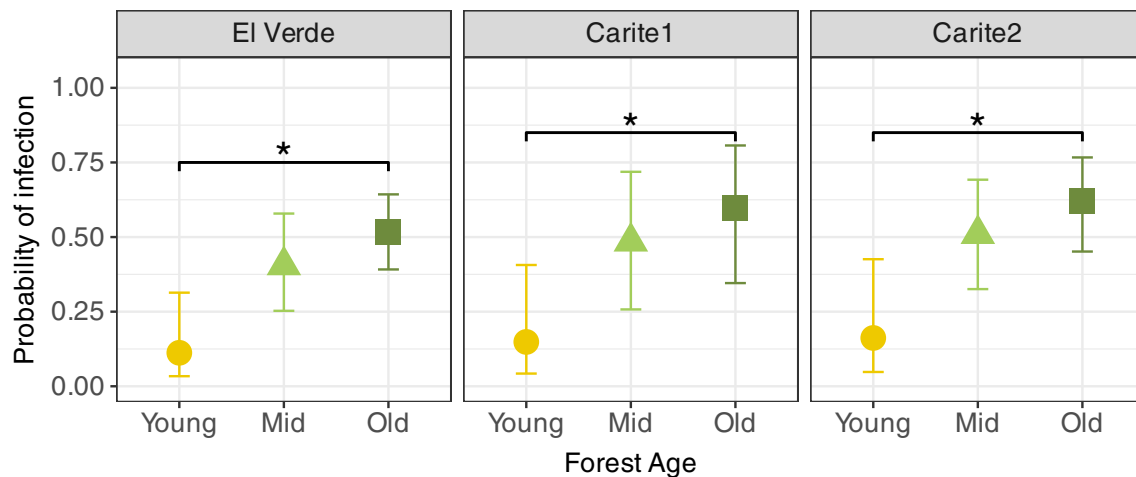
FIGURE 3 The figure shows model predictions of probability of malaria infection in males and females *Anolis gundlachi* among three forest ages in El Verde, Carite1 and Carite2. Large symbols and error bars represent mean and 95% CI from a generalized linear model with binomial distribution and logit link function. Brackets emphasize clear statistical differences among forest ages (one asterisk represents $p < 0.05$). For simplicity, the figure shows average predictions among adult males, and females. Overall, the model predicts low probability of parasite infection in the young forest compared with the old forest.

high prevalence of dispersive traits, less density dependence, and escape and release of parasites in younger forests compared with old-growth forests. Our results show support for the three predictions. We found lower abundance and lower parasitism prevalence in young forests compared with old forests consistent among sites. Nevertheless, we found support for the hypothesis of changes in phenotypic traits only in some sites suggesting that, for these traits, local effects may be particularly important.

Individuals were larger in the young forest in El Verde, but the pattern was the opposite in Carite1. Body size in anoles is correlated with various ecological and functional traits (Losos, 2009). Older adults tend to

be larger (Stamps, 1983) and one potential explanation is that these differences in size ultimately reflect population-level differences in age. Because there is a peak in breeding in the summer, this would have been a plausible explanation if forests of different ages were surveyed in different seasons (e.g., young forest in the winter, and old-growth forest in the summer). However, we surveyed forest of different ages within the same site in the same week to control for these potential ontogenic changes. Alternatively, a high prevalence of larger anoles in the young forest in El Verde and old forest in Carite1 could be the result of lower rates of predation or overabundant prey driving higher individual growth rates

(Roughgarden & Fuentes, 1977). Birds are the most important predators of anoles in the Caribbean (Wunderle Jr, 1981). While there is evidence of variation in predation rates among islands or among habitats (McLaughlin & Roughgarden, 1989), within the same forest type there is little evidence of large variations in bird species composition (Acevedo & Restrepo, 2008) leading to differences in predation rates. The frequency of anoles' tail loss has been used as an index of predation rates (e.g., Bateman & Fleming, 2011). We conducted an ad-hoc analysis of tail loss that shows no clear evidence of differences in the probability of having a broken or regenerated tail among forest ages or sites (Appendix S1: Table S10). In terms of prey abundance, lizards are opportunists and can feed on a wide variety of prey (e.g., Simmonds, 1958). Still, ants are their most common prey item in the West Indies (Reagan, 1986). Maximum prey size increases with body size, therefore, larger individuals can capitalize on a more varied diet (e.g., Whitfield & Donnelly, 2006) which could be advantageous when colonizing novel environments. While, in Puerto Rico, forests of 25–35 years are characterized as having a higher species richness of insects (Osorio-Pérez et al., 2007), this pattern is highly variable (Barberena-Arias & Aide, 2002). Therefore, a plausible hypothesis is that prey availability was not necessarily correlated with forest age in these chronosequences. Last, low density of conspecifics can ultimately result in larger individuals on average due to an increase in the per-capita availability of prey (Schoener, 1969). While we did not have density data for Carite1, our results showing lower densities in young forests in El Verde support this hypothesis (see below).

We found that individuals generally had smaller forelimbs in the young forest in El Verde, but we found the opposite pattern in Carite2. Limb sizes in anoles are a plastic trait that responds strongly to habitat structure (Losos et al., 2000). For instance, in *Anolis. sagrei* and *A. carolinensis* there is a strong correlation between relative hindlimb length and perch diameter (Calsbeek & Irschick, 2007). When these species were raised in cages with broad surfaces, they developed longer hindlimbs relative to their body size (Kolbe & Losos, 2005). Our results show statistical differences in forelimbs (radius/ulna and humerus) among forest ages, but no clear differences in hindlimbs (tibia and femur). Hindlimbs are used for propulsion and are a key determinant of sprint speeds (Losos & Irschick, 1996). While higher sprint speeds promote better antipredator responses, sprint speeds usually decline with decreasing perch diameter (Irschick & Losos, 1999), and anoles with long legs often stumble or fall more often when navigating narrow surfaces (Losos & Sinervo, 1989). Still, our results emphasize variations in the size of forelimbs and not hindlimbs. Our overall understanding of the role of forelimbs in anoles is more limited (Foster & Higham, 2012). One of the few studies on the contrasting roles of forelimbs and hindlimbs shows that in the presence of small perches—typical of recovering and young forests—forelimbs and hindlimbs show opposite kinematics (Foster & Higham, 2012). Also, in the presence of smaller perches, forelimbs are more functionally plastic, have a greater range of motion, and contribute more to propulsion. Therefore, having smaller forelimb sizes can be optimal in habitats with smaller perches. In El Verde, we found a higher prevalence of longer forelimbs in the young forests which are characterized by having smaller trees (Figure 4a). While smaller trees are not necessarily a trait traditionally associated with older forests, in Carite2 the old and mid forests were characterized for also having a high prevalence of smaller trees (Figure 4a). This is because these forests were in mountain ridges that were severely damaged by Hurricane Maria in 2017. Many of the bigger trees broke and smaller trees emerged during hurricane recovery. In contrast, the young forest in Carite2 was in a valley protected from wind damage by the nearby mountains. Moreover, forest structure of patches with similar ages may vary due to other factors such as soil properties and past land-use types (e.g., cattle ranching vs. crops). Therefore, even though we found differences in forelimb sizes these may not necessarily represent highly dispersive traits as predicted by range expansion theory but are likely a plastic response to habitat structure.

We found a lower density of individuals in young forests and this result was consistent in El Verde and Carite2. Multiple nonmutually exclusive hypotheses may explain this consistent pattern. As predicted by range expansion theory, these low abundances may be the result of small initial recolonizing populations. These small populations may still be undergoing density-independent growth. This hypothesis is supported by our finding of higher population growth rates in the young forest in El Verde compared with the old-growth forest. Still, there are other nonmutually exclusive alternative hypotheses that may also explain this low abundance in young forests. First, *A. gundlachi* habitats have relatively lower temperatures when compared with other forest types in Puerto Rico. This species is a thermocomformer which means that they do not regulate their body temperatures using behaviors like basking (Huey & Webster, 1976). Young forests had consistently higher substrate temperatures among all chronosequences (Figure 4b). Therefore, their low density may be the result of young forests providing suboptimal habitat for their temperature requirements. Also, while young forests often have some large trees likely remnants from previous old-
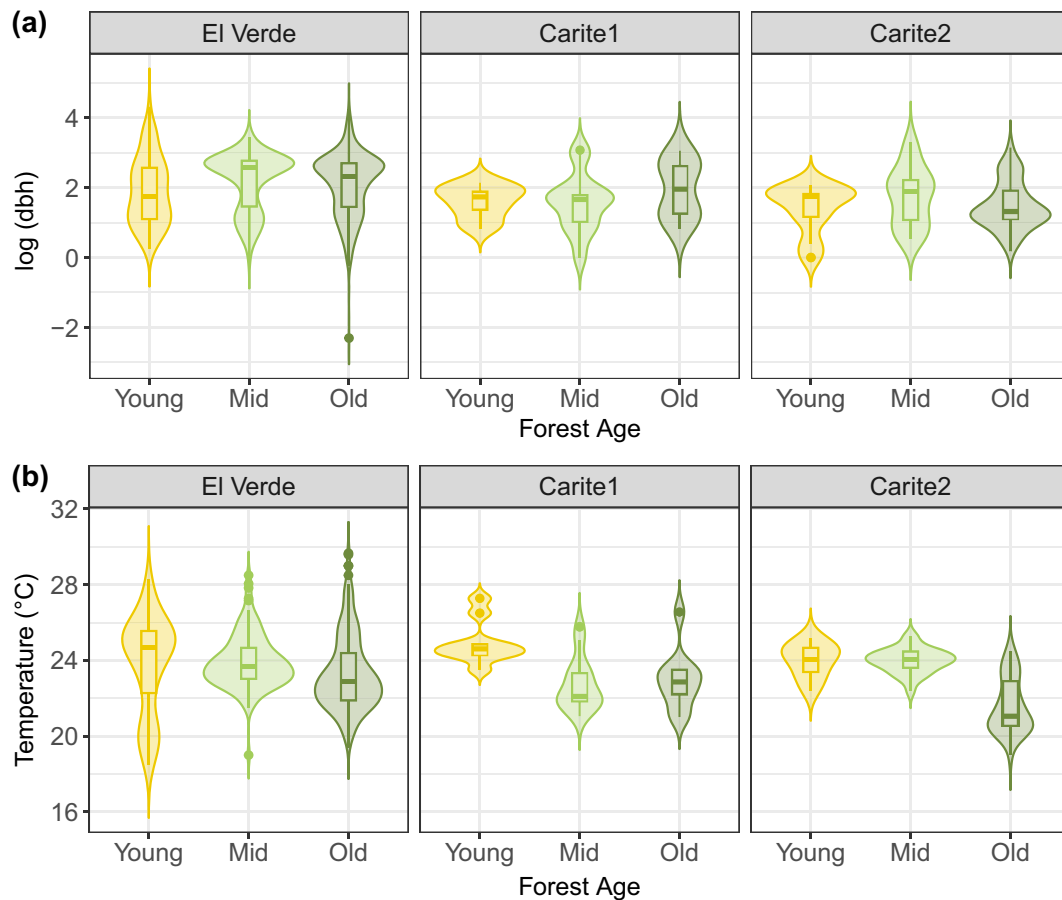
FIGURE 4 The figure shows the distribution of (a) substrate temperatures and (b) substrate size (i.e., diameter at breast height: dbh) among forest ages and sites. Note that substrate size is shown in the log scale. Overall, temperatures are higher, on average, in the young forests when compared with the old forests. In El Verde the distribution of substrate sizes shows a higher prevalence of larger substrates in old and mid forests compared with the young forest. In contrast, in Carite2 the young forest has a higher relative prevalence of larger substrates when compared with the old forest. In Carite1 the distributions are similar with a slight higher prevalence of larger substrates in the old forests.

growth forests, they are characterized for having smaller trees and a complex understory of vines, shrubs and other herbaceous vegetation (e.g., Herrera-Montes & Brokaw, 2010; Rios-López & Mitchell Aide, 2007). Therefore, in young forests *A. gundlachi* is not the only anole using the understory of the forest. Instead, it must also compete with *A. krugi* and *A. pulchellus*, who are ecomorphs adapted to these early successional habitat conditions. This competition may also result in lower densities compared with old forests where these other species of anoles are rare in the understory. Last, the low density of individuals may also be the result of a limited number of high-quality substrates. Large trees, which are the preferred substrate, are limited in young forests and often colonized by large and dominant males. Therefore, in addition to initial small population sizes, suboptimal habitat characteristics (higher temperatures and lower number of substrates) and increased interspecific and intraspecific competition may interact in complex ways to ultimately result in low population densities.

Our results also support the prediction of lower rates of parasitism in the young forests and this result was consistent among forest types. Vector-borne parasite transmission is a complex process mediated by host and vector densities, and their interaction (Smith et al., 2012). Our results show that host density is lower in the younger forests which can partially explain the lower parasitism rate, as predicted by range expansion theory. The vector of lizard malaria in Puerto Rico is currently unknown, but our research group has identified a Culex mosquito species as a likely vector (Reeves et al., unpublished). This group of mosquito vectors breeds mostly on bromeliads and heliconia flowers which are less common in the young forests. Therefore, in addition to having initially fewer imported infections as predicted by range expansion theory, the low availability of vector breeding habitats may also explain the low parasitism rate.

The results from this study are contingent on assumptions common to other chronosequence studies. For instance, space-for-time substitution in chronosequence

studies assumes that spatial and temporal variations are equivalent (Pickett, 1989). This is a plausible assumption if there is evidence that sites of different ages follow a similar trajectory (Walker et al., 2010). Comparisons between biodiversity patterns inferred from chronosequences and the pollen record have been found to be highly accurate (e.g., Blois et al., 2013). Still, other studies emphasize caution, particularly in sites where there is rapid species turnover (Johnson & Miyanishi, 2008). There have been multiple chronosequence studies conducted in Puerto Rico to describe patterns of forest recovery (e.g., Aide et al., 1995, 1996; Rivera & Aide, 1998), largely because the key assumptions of space-for-time substitutions are met. Forests of different ages coexist in close proximity which helps control for multiple confounding factors.

All in all, our results show support for range expansion theory as an appropriate framework to describe fauna recolonization of recovering forests. This is particularly true for predictions on density, population growth rates, and parasitism. It is possible that more rigorous criteria for site selection obscured findings regarding morphometrics. Still, our results showing variability in phenotypic trait patterns among sites emphasize the trade-off between dispersive traits and others that improve their likelihood of establishing in novel areas (Baguette & Van Dyck, 2007). A similar result was observed during experimental introductions of *A. sagrei* in Staniel Cay in the Bahamas. After 20 years, the population diverged nonrandomly from the source population showing traits that responded to vegetation and habitat likely resulting from plasticity rather than genetic differentiation (Campbell & Echternacht, 2003; Losos et al., 2001). This trade-off between dispersive traits and adaptations to the new environment will depend on the time since initial recolonization. Dispersive traits will be advantageous during initial colonization, but as time progresses, other adaptations to novel conditions will be more important than dispersive traits. Here we observed patterns in the population at least 20–30 generations since the initial recolonization (assuming 1 year generation time) which for anoles who are highly plastic is enough time to show differentiation at least in phenotypic traits. An assessment of the patterns and processes during the initial stages of recolonization through a field experiment would be an appropriate next step.

While range expansion's theoretical framework proved useful to understanding anoles recolonization of secondary forests, our results also emphasize that the processes that drive fauna recolonization are complex and nuanced. Empirical support for range expansion theoretical predictions comes mostly from invasive species (Hastings et al., 2005). Although there are similarities between the process of invasion and recolonization, there

are some important differences. First, the introduction of nonnative species is often related to human activities, while native species' range expansion is, in many instances, driven by environmental factors such as natural regeneration or global climate change. Second, native species may share an evolutionary history with their colonizing sites. This includes adaptations for environmental conditions and co-evolved natural enemies. These co-evolved natural enemies are often absent in invasive species expansions. Third, recovering habitats are recolonized by source populations in close proximity, potentially synchronizing population dynamics and facilitating a bridge of gene flow that improves adaptability to the colonizing environment. Regardless of these key differences, finding support for range expansion predictions in our study is an encouraging first step.

AUTHOR CONTRIBUTIONS

MAA, CF, and RP conceived and designed the study. MAA, CF, LG, BG, and MQ collected the data. MAA analyzed the data. MAA and RP acquired the funding for this project. MAA wrote the manuscript. All authors contributed critically to the drafts and approved the final manuscript.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Acevedo et al., 2024a) are available in Dryad at https://doi.org/10.5061/dryad.jwstqjqgm. The code used for statistical analyses (Acevedo et al., 2024b) is available in Zenodo at https://doi.org/10.5281/zenodo.10542428.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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