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THE ROYAL SOCIETY PUBLISHING

Ectoparasite extinction in simplified lizard assemblages during experimental island invasion

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Introduced species can become invasive, damaging ecosystems and disrupting economies through explosive population growth. One mechanism underlying population expansion in invasive populations is 'enemy release', whereby the invader experiences relaxation of agonistic interactions with other species, including parasites. However, direct observational evidence of release from parasitism during invasion is rare. We mimicked the early stages of invasion by experimentally translocating populations of mite-parasitized slender anole lizards (Anolis apletophallus) to islands that varied in the number of native anoles. Two islands were anole-free prior to the introduction, whereas a third island had a resident population of Gaige's anole (Anolis gaigei). We then characterized changes in trombiculid mite parasitism over multiple generations post-introduction. We found that mites rapidly went extinct on one-species islands, but that lizards introduced to the two-species island retained mites. After three generations, the two-species island had the highest total density and biomass of lizards, but the lowest density of the introduced species, implying that the 'invasion' had been less successful. This field-transplant study suggests that native species can be 'enemy reservoirs' that facilitate co-colonization of ectoparasites with the invasive host. Broadly, these results indicate that the presence of intact and diverse native communities may help to curb invasiveness.
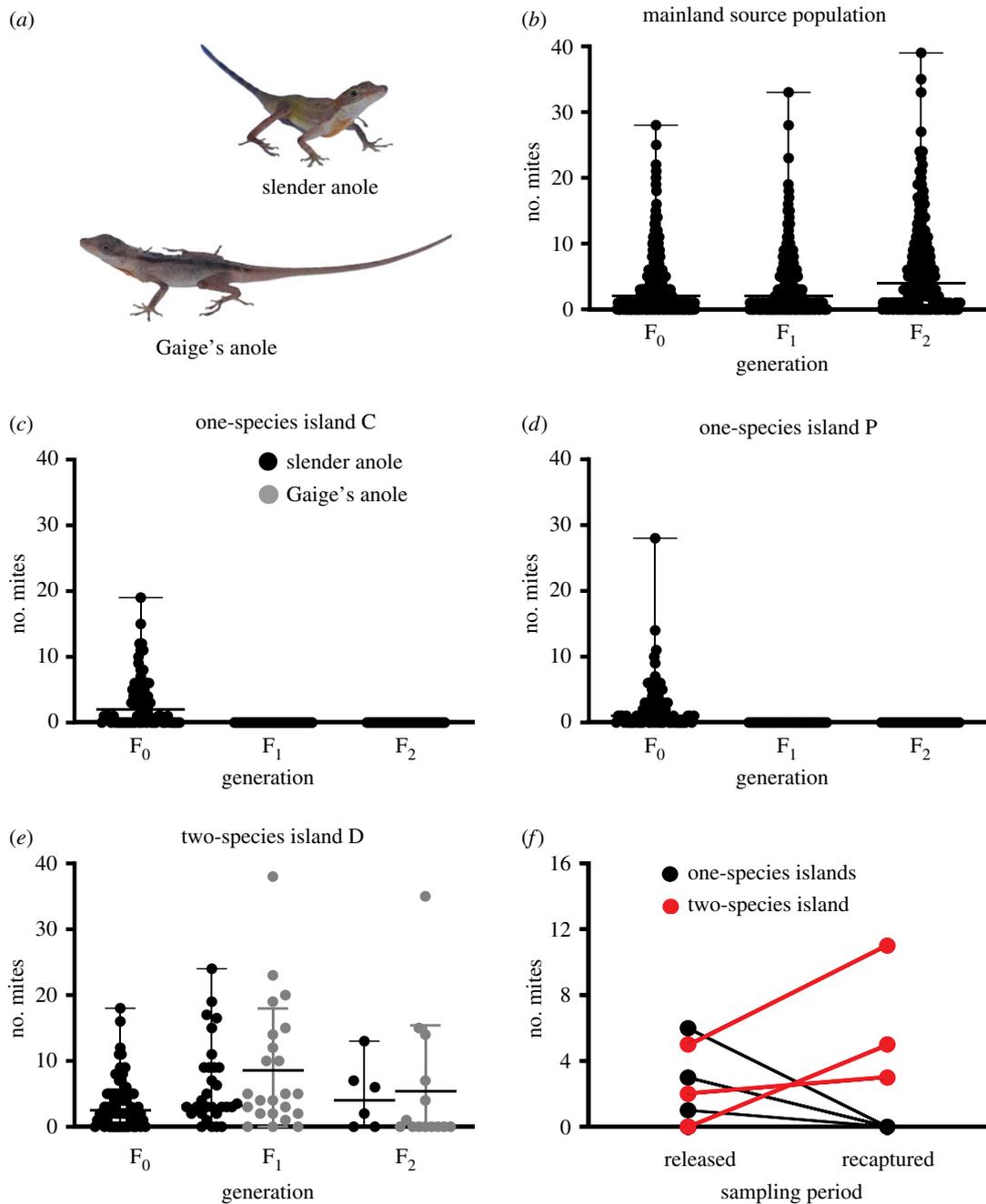
Figure 1. Changes in the number of mites within and among generations for populations and individual founder lizards. (*a*) Slender anole (*Anolis apletophallus*) and Gaige's anole (*A. gaigei*). Photos by John David Curlis. Total number of mites on slender anole lizards for the mainland (*b*), islands with one species (*c,d*) and two species (*e*) in the founding generation (F_0) and two successive generations (F_1 and F_2). Lines indicate medians and range. Mites disappeared from all lizards on one-species islands (*a,b*) but persisted for three generations on the two-species island (*c*). (*f*) Initial and final numbers of mites in individual founder lizards that persisted on islands for multiple years (each line represents an individual lizard). Founding individuals invariably lost all mites on one-species islands but retained or gained mites on the two-species island.

1. Introduction

Humans are rapidly homogenizing the world's biota by transporting species around the globe [1–4]. Some introduced species have become invasive, wreaking great damage to ecosystems [5–12] and impacting agricultural and natural extractive industries to the tune of millions of dollars per year [13–16]. Indeed, the impact of invasive species is predicted to become increasingly dire in the context of global change [17–19]. A common feature of invasive species is rapid population expansion following initial colonization [20–24], which has been linked to ecological release from previous sources of population regulation. Explosive population growth can result from reduced interactions with predators [25], competitors [26] and parasites [27–29]—a process termed 'enemy

release' [30–33]. In particular, many non-native species experience either reduced or absent parasites post-introduction, and this seems to enhance their ecological dominance [27–29,34]. Previous studies that have observed parasite loss during invasion have tended to be observational in nature [27–29,35] and were conducted after species became established or invasive during the generations after initial colonization [27–29,35,36]. However, experimental support for enemy release during biological invasions is rare [33,37]. Thus, the timescale and specific factors that regulate parasite persistence or loss during the early stages of invasion remain poorly understood.

We used a field-transplant experiment to examine the impact of the presence of a native congener on the dynamics of ectoparasite infections in the colonization stage of replicated biological invasions. We experimentally introduced
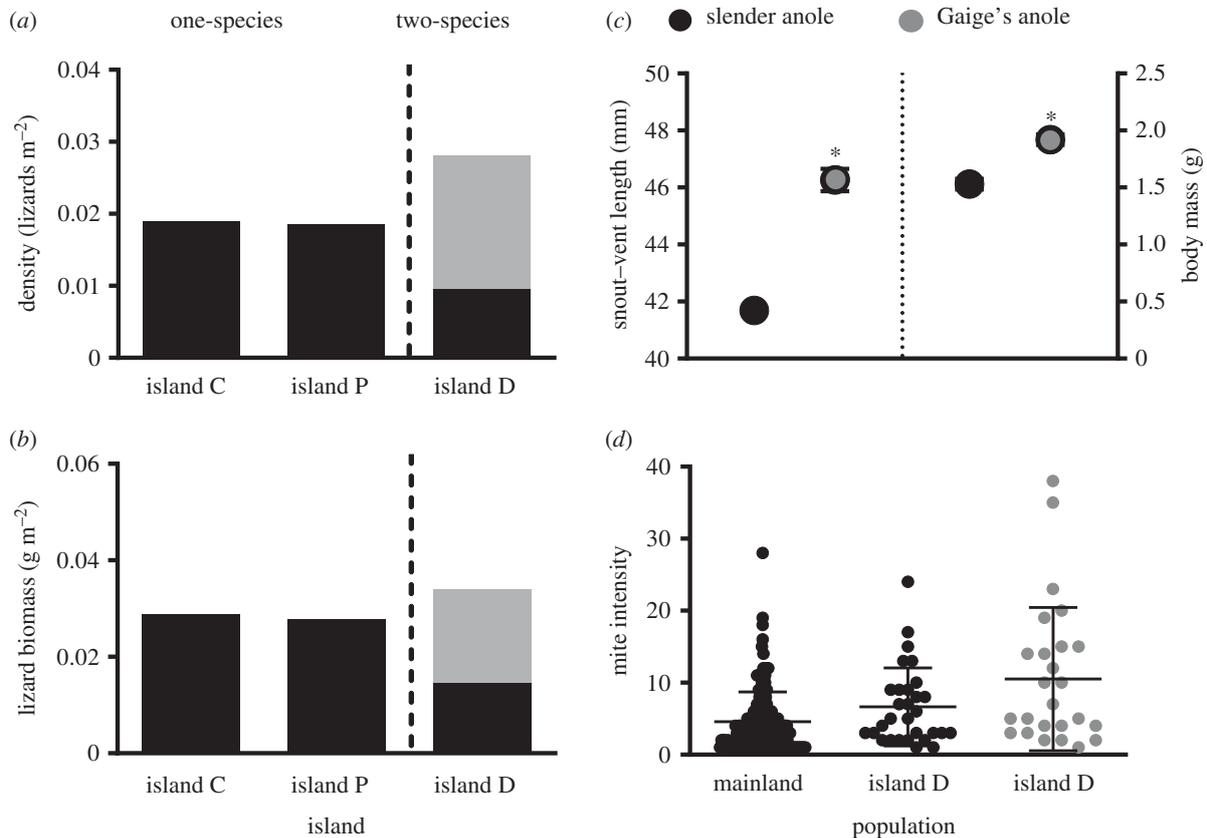
Figure 2. Density and biomass of lizards on each island, as well body size and parasitism of Gaige's anoles. Density of lizards (*a*) and lizard biomass (*b*) on islands, based on mark recapture over three lizard generations. Mites persisted only on a two-species island with high total lizard density and biomass per unit area. (*c*) Body length and body mass of slender and Gaige's anoles on the two-species island (island D), the island where mites persisted. Symbols indicate mean ± SEM. (*d*) Intensity of mite infection on the source (mainland) population of slender anoles, and both slender and Gaige's anoles on island D. Lines indicate median and range. Gaige's anoles, which are longer and heavier than slender anoles, had significantly higher intensity of parasitism than slender anoles from the mainland, suggesting that they may have served as a reservoir of parasitism during the slender anole invasion.

Panamanian slender anoles (*Anolis apletophallus*; hereafter, 'slender anoles') to islands that varied in lizard community structure in Lake Gatún (Panama Canal), Panama, so that we could follow ectoparasitism in the generations immediately following colonization. Lake Gatún was formed as a man-made reservoir during the construction of the Panama Canal [38]. As the Chagres River was dammed around the turn of the twentieth century, the Chagres Valley was flooded to form the lake, isolating hundreds of hilltops into small islands [38]. We used these islands as a natural system by which to replicate the colonization stage of biological invasions. Numerous species of anole lizards have been introduced outside of their native range and have become invasive [39–43]. We chose slender anoles because they are abundant, can be readily recaptured and have short generation times (approx. 9 months) [44]. Further, slender anoles in central Panama are often parasitized by the trombiculid mite *Eutrombicula dugesii*, which attaches to the integument of the lizard and uses a feeding tube called a stylosome to digest and consume lizard scales, skin and interstitial fluid. These ectoparasite infections in lizards can cause integumental lesions [45,46], alter social and thermoregulatory behaviour [47,48], decrease growth and body condition [47,49] and act as vectors for diseases [50].

2. Material and methods

We captured 210 adult slender anoles (figure 1*a*) from Soberanía National Park on mainland Panama, measured several

morphological traits and counted mite loads via visual inspection (electronic supplementary material). We then gave each individual a unique tag using visible implant elastomers and released them across three islands (70 lizards per island, equal sex ratios) in July and August of 2017 (see electronic supplementary material). While abiotic conditions on islands were generally similar (see electronic supplementary material), one island had a resident population of Gaige's anole (*Anolis gaigei*), whereas the other two did not have a resident anole prior to the introduction of slender anoles. Gaige's anoles (figure 1*a*) are likely competitors of slender anoles, with broad overlap in body size, diet and microhabitat use [51,52].

3. Results and discussion

Slender anoles on the mainland retained mite infections for the duration of the study, and median abundance of mites actually increased over the three years of the study (figure 1*b*). However, mark recapture studies over the following 2 years revealed that mites went extinct on both one-species islands after a single generation and remained absent into the third generation (figure 1*c,d*). Indeed, every mite-infested founder individual (electronic supplementary material) on the one-species islands that we recaptured in the first year subsequently lost all their mites. Thus, mites were lost very rapidly within the first generation (figure 1*f*). By contrast, the slender anole population transplanted to the island with the native Gaige's anole remained infected with mites into the third generation (figure 1*e*). Moreover, many of the

founding individuals on the two-species island actually gained mite infections (figure 1*f*). Given the high rates of ectoparasitism that we observed on Gaige's anoles, it is likely that the native island population of this species was infected with mites prior to the introduction of slender anoles. Total lizard density and biomass per unit area of both species were highest on the two-species island (electronic supplementary material), implying that mites might only be able to persist in relatively dense lizard populations (figure 2). However, the two-species island had the lowest density and biomass per unit area of non-native slender anoles, and the density of slender anoles negatively covaried ($p < 0.001$) with the density of Gaige's anoles (electronic supplementary material) [53]. These results are consistent with either the negative impact of parasites or interspecific competition on lizard population size, and these factors are not mutually exclusive (figure 2). Mites might also have persisted on the two-species island because Gaige's anole was a potentially superior host (electronic supplementary material). Gaige's anoles were larger in both body length ($p < 0.0001$) and mass ($p < 0.0001$) than slender anoles, which provides greater surface area for attachment (figure 2). Indeed, the intensity of mite infection (number of mites on infected individuals) was significantly greater ($p < 0.0001$) for Gaige's anoles on island D than for slender anoles from the mainland source population (figure 2). Furthermore, infection prevalence was greater for the slender anole population on the two-species island than in the mainland source population ($p = 0.0301$).

We found that ectoparasitic mites on slender anoles were rapidly extirpated on single-species islands despite increasing in abundance during the same period in the mainland source population. However, mites persisted for three generations on the two-species island. Our results imply that the presence of a highly parasitized native species might facilitate greater parasite prevalence and intensity of infection in the introduced species, and this is likely to reduce the fitness and ecological impact of the invader. Broadly, our data highlight the importance of community structure for enemy release during the colonization stage of biological invasions. Biological communities that are phylogenetically similar to the community of the invader may be more resistant to invasion [54,55], perhaps because either the invader or native species can serve as alternative hosts to endemic or invading parasites. Conversely, previous work has noted that evolutionarily distinct communities found on islands and other isolated land masses are especially vulnerable to biological invasions, because reduced phylogenetic similarity between invasive species and the invaded community would facilitate enemy release from ectoparasites and other enemies [5,20,56]. Given the ubiquity and diversity of invasive species, one important implication of this research is that more diverse native communities can function as reservoirs of parasitism that could ultimately help to curb invasiveness.

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