

Pervasive and persistent effects of ant invasion and fragmentation on native ant assemblages

RAFAEL ACHURY ^{1,4,5} DAVID A. HOLWAY,² AND ANDREW V. SUAREZ^{1,3}

¹Department of Entomology, University of Illinois at Urbana-Champaign, 320 Morrill Hall, 505 S. Goodwin Avenue, Urbana, Illinois 61801 USA

²Division of Biological Sciences, University of California at San Diego, La Jolla, California 92093 USA

³Department of Evolution, Ecology and Behavior, University of Illinois at Urbana-Champaign, Urbana, Illinois 61801 USA

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Abstract. Biological invasions are a leading cause of global change, yet their long-term effects remain hard to predict. Invasive species can remain abundant for long periods of time, or exhibit population crashes that allow native communities to recover. The abundance and impact of nonnative species may also be closely tied to temporally variable habitat characteristics. We investigated the long-term effects of habitat fragmentation and invasion by the Argentine ant (*Linepithema humile*) by resurveying ants in 40 scrub habitat fragments in coastal southern California that were originally sampled 21 yr ago. At a landscape scale, fragment area, but not fragment age or Argentine ant mean abundance, continued to explain variation in native ant species richness; the species–area relationship between the two sample years did not differ in terms of slope or intercept. At local scales, over the last 21 yr we detected increases in the overall area invaded (+36.7%, estimated as the proportion of occupied traps) and the relative abundance of the Argentine ant (+121.95%, estimated as mean number of workers in pitfall traps). Argentine ant mean abundance also increased inward from urban edges in 2017 compared to 1996. The greater level of penetration into fragments likely reduced native ant richness by eliminating refugia for native ants in fragments that did not contain sufficient interior area. At one fragment where we sampled eight times over the last 21 yr, Argentine ant mean abundance increased over time while the diversity of native ground-foraging ants declined from 14 to 4 species. Notably, native species predicted to be particularly sensitive to the combined effect of invasion and habitat loss were not detected at any sites in our recent sampling, including the army ant genus *Neivamyrmex*. Conversely, two introduced ant species (*Brachymyrmex patagonicus* and *Pheidole flavens*) that were undetected in 1996 are now common and widespread at our sites. Our results indicate that behaviorally and numerically dominant invasive species can maintain high densities and suppress native diversity for extended periods.

Key words: ant abundance; Argentine ant; biological invasions; ecological impacts; habitat loss and fragmentation; *Linepithema humile*; long-term dynamics; native communities; southern California.

INTRODUCTION

The abundance and diversity of natural populations are under threat from mechanisms including habitat loss and fragmentation, biological invasions, pollution and climate change, disease, and overexploitation (Tilman et al. 2017). These factors do not work in isolation and synergies among them are common. For example, both habitat fragmentation and climate change may facilitate the establishment and spread of biological invasions (Stachowicz et al. 2002, With 2002, Didham et al. 2007, Ricciardi 2007, Bellard et al. 2013). Interactions among

causative agents of biodiversity loss make it difficult to pinpoint specific strategies for management and conservation plans. For example, despite a strong association between land use and invasion prevalence, the relative contribution of each to biodiversity loss is not always clear (Brown and Gurevitch 2004, Didham et al. 2005, King and Tschinkel 2008, Pyšek et al. 2010).

Habitat loss and fragmentation have pervasive impacts on biodiversity and ecosystem function (Ewers and Didham 2006, Resasco et al. 2016, Fletcher Jr et al. 2018). Consequences of fragmentation arise from a loss of total area, increased isolation of remaining patches, and exposure to edge effects that initiate long-term changes in the structure and function of the species assemblages remaining in fragments (Haddad et al. 2015, Hertzog et al. 2019). Responses to fragmentation include reduced persistence within smaller fragments and decreased colonization of more isolated patches of

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Corresponding Editor: Kathryn L. Cottingham.

⁴Present address: Terrestrial Ecology Research Group, Department of Ecology and Ecosystem Management, Technical University of Munich, Freising, 85354 Germany

⁵E-mail: rafaalachury@gmail.com

habitat, thus lowering the rate of recolonization after extinction (Holt et al. 1995). Additionally, fragmented landscapes contain a higher proportion of edge for a given amount of habitat (Fahrig 2003); this geometric relationship alters abiotic conditions (Haddad et al. 2015) and can promote penetration by introduced species (Brothers and Spingarn 1992, Suarez et al. 1998, Malavasi et al. 2014), further altering species richness and persistence of native biodiversity over time (Fischer and Lindenmayer 2007).

Most ecosystems are vulnerable to invasion to some degree (Lowry et al. 2013), but the long-term consequences of invasion are often unknown (Simberloff and Gibbons 2004, Yelenik and D'Antonio 2013). Research on the effects of invaders is often conducted over short periods of time or involves comparisons of invaded and uninvaded sites at a single time point (Strayer 2012). Studies that follow invasion dynamics over longer periods have reported reductions in invasion impacts commensurate with declines in invader abundance (Morrison 2002, Simberloff and Gibbons 2004, Lester and Gruber 2016). For example, when a species spreads into a new environment, it may have an acute phase with rapid population growth and range expansion that is accompanied by a large impact on the native ecosystem (Strayer et al. 2006). A chronic phase may follow where invader abundance and impact decline due to accumulation of enemies (Diez et al. 2010, Wardle et al. 2011), evolutionary changes within the invaded community (Mooney and Cleland 2001, Phillips and Shine 2004), or population regulation resulting from density-dependent factors. In contrast, the abundance and impacts of introduced species can also persist long after introduction (D'Antonio et al. 2011, Sharpe et al. 2017, Menke et al. 2018), with control and management necessary to restore native communities.

Native to northern Argentina and surrounding regions, the Argentine ant (*Linepithema humile*) is a widespread invader with established populations on five continents and many oceanic islands (Suarez et al. 2001, Wetterer et al. 2009). The success of the Argentine ant has been related to its numerical dominance, collective competitive ability, increased aggression, and foraging efficiency (Human and Gordon 1996, Holway 1999, Human and Gordon 1999, Holway and Case 2001). In introduced populations, Argentine ants displace native ants, altering ant community composition and disrupting seed dispersal and pollination mutualisms (Bond and Slingsby 1984, Christian 2001, Holway et al. 2002a, Carney et al. 2003, Hanna et al. 2015). However, we know relatively little about how their abundance and the impacts associated with invasion change over time. In urban areas in New Zealand, for example, populations of *L. humile* have declined, apparently allowing native ants to recover (Cooling et al. 2012). Conversely, in California, Argentine ants have persisted in many areas with little evidence that ant communities have recovered from diversity loss and homogenization attributed to the

invasion (Human and Gordon 1996, Holway and Suarez 2006, Vonshak and Gordon 2015, Menke et al. 2018).

We resurveyed ant assemblages in 40 habitat fragments and an unfragmented reserve of scrub habitat in coastal southern California to examine how invasion and habitat fragmentation affect native ant assemblages through time. Specifically, we used ant community composition measured at sites sampled 21 yr apart to evaluate the following general questions: (1) Is native ant species richness predicted by the same fragment-level variables as it was 21 yr ago (specifically fragment size, age, and Argentine ant mean abundance)? (2) Have the distribution and relative abundance of Argentine ants changed between sampled periods? (3) Do native ants show signs of recovery or have the combined effects of fragmentation and invasion continued to cause declines in ant diversity? We also compared the species–area relationships between 1996 and 2017 for evidence supporting one of four predicted outcomes of the long-term effects of habitat fragmentation and invasion on native ant diversity (Fig. 1): native species will be lost across all fragments in equal proportions due to stochastic processes (Fig. 1a); larger fragments that had low occupancy of Argentine ants in 1996 should experience a greater loss of native ant species if the Argentine ant continued to spread or increased in abundance (Fig. 1b); native ant species may recover in fragments if Argentine ants have declined or been lost from fragments and recolonization has taken place in the last 20 years (Fig. 1c); if the effects of invasion and fragmentation are consistent, the species–area relationship should remain similar through time (Fig. 1d).

METHODS

Study system

All fragments and plots within the unfragmented reserve sampled in this study are located in coastal sage scrub and chaparral habitat in San Diego County, California, USA. Numerically dominant perennial plant species include California buckwheat (*Eriogonum fasciculatum*), California sagebrush (*Artemisia californica*), laurel sumac (*Malosma laurina*), lemonade berry (*Rhus integrifolia*), and *Opuntia littoralis* (Cleland et al. 2016). The greatest impact on coastal sage scrub both historically and today has been habitat loss from urbanization (Soulé et al. 1988, Chen et al. 2010). In the San Diego region, urban development along the coast has occurred primarily on mesa tops and level expanses, resulting in isolated fragments of natural vegetation mostly consisting of narrow, steep-sided canyons of different sizes. This process has served as a unique opportunity to understand the effects of habitat loss and fragmentation on a variety of organisms, including birds (Soulé et al. 1988, Crooks et al. 2004), small mammals (Bolger et al. 1997), carnivores (Crooks and Soulé 1999), ants (Suarez et al. 1998), bees (Hung et al. 2019),

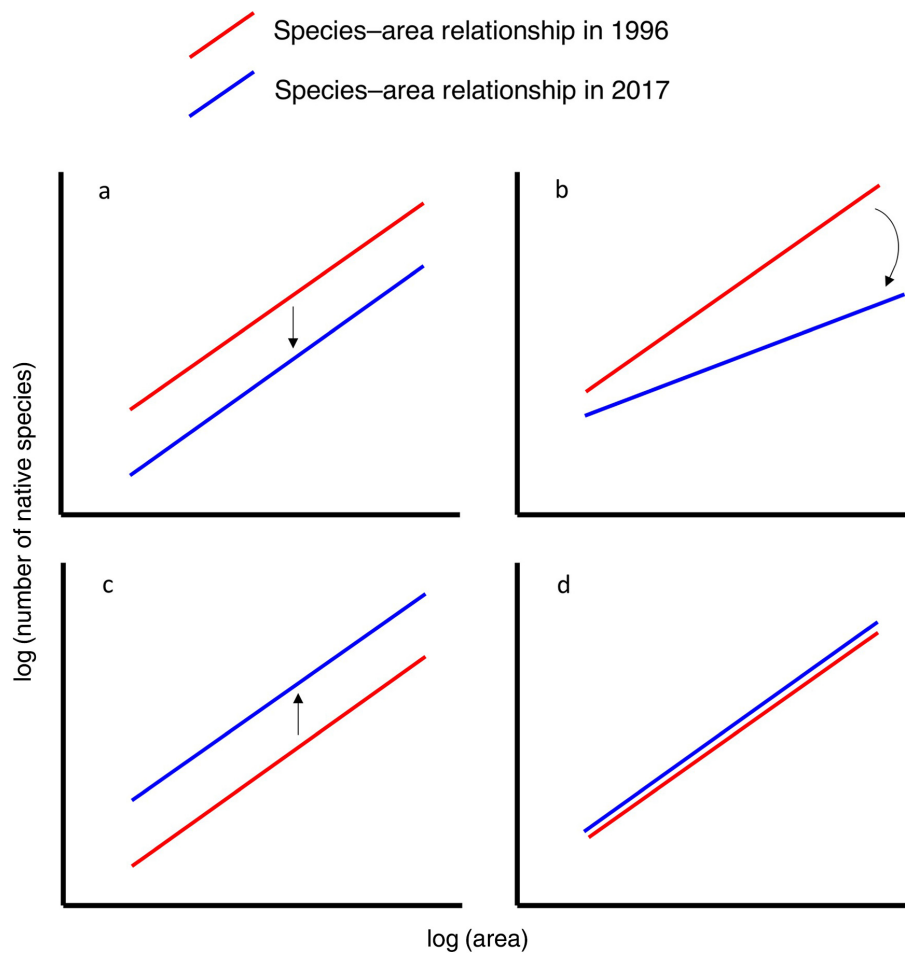


FIG. 1. Potential examples of how species–area relationships might be affected by the long-term effects of invasion and fragmentation. (a) The number of species increases with area, but there is a reduction of native species after 21 yr (different intercepts) without apparent change in the rate of loss (same slopes). (b) The number of species does not vary in smaller fragments (same intercepts), but the rate of loss of native species through time is more dramatic in bigger fragments (different slopes). (c) The number of species increases with area and the native species rebound after 21 yr (different intercepts) without apparent change in the rate of gains (same slopes). (d) The number of native species increases with area, but neither the diversity within fragments nor the rate differs after 21 yr (same intercepts and same slopes).

arthropods (Bolger et al. 2000), and plants (Alberts et al. 1993).

We examined long-term effects of invasion and fragmentation by resampling the ant assemblages present in 40 habitat fragments and 10 plots of different sizes in continuous unfragmented expanses of scrub habitat (Appendix S1: Fig. S1a and Table S1). The 10 plots within continuous habitat ranged from 2.81 to 86.78 ha in size, resembling the area and topography of the fragments, and were located in and adjacent to the University of California Elliott Chaparral Reserve. The Elliott Reserve covers an area of 74 ha and is nested within the Marine Corps Air Station Miramar, which includes ~9,000 ha of undeveloped land. For each fragment, we recalculated the same descriptors that were measured in 1996 including (1) size, (2) time since isolation by urban development, (3) distance to the nearest expanse of

unfragmented habitat (i.e., degree of isolation), and (4) irregularity (i.e., the ratio of area to perimeter for each habitat fragment; Appendix : Table S1). Values for these descriptors were obtained from Google Earth satellite images (accessed in May 2018; imagery data: 8 December 2017), except for time since isolation, which was obtained from Suarez et al. (1998). Time since isolation, or the “age” of the fragment, ranged from 3 to 95 yr in 1996, and 24–116 yr in 2017. The degree of isolation represents the distance between each fragment and the nearest core area that contained native ant species (Core areas: Marine Corps Air Station Miramar, Proctor Valley, Otay Valley, Cabrillo National Monument and Carmel Mountain; see Suarez et al. [1998] for detailed description). Finally, we combined data obtained in 2017 with data from repeated sampling of a single fragment (Rice Canyon), which was sampled seven times

from 1996 to 2003, to examine patterns of ant diversity and mean abundance at a finer temporal scale (see also Tillberg et al. 2007).

Sampling

Since our main goal was to examine changes in the effects of invasion, habitat loss and fragmentation on ant communities between two summers 21 yr apart, we made every effort to sample ants with the exact same protocols implemented in Suarez et al. (1998). We used pitfall traps to estimate native ant species richness and the mean abundance of the Argentine ant. Both studies employed the same type of pitfall trap and the same sampling effort, at the same locations and time of year. In each fragment we placed an array of five pitfall traps every 100 m along a transect corresponding to the fragment's longest axis; the number of arrays varied depending on fragment or plot size (Appendix S1: Table S1 and Fig. S1b). Arrays placed in plots within the unfragmented area were also aligned along linear transects. The placement of pitfall traps in each array conformed to a pattern resembling the five on a die with 20 m between traps on each corner and a fifth trap in the center. Pitfall traps each consisted of 240-mL glass jars, 73 × 89 mm (Qorpak, Bridgeville, Pennsylvania, USA), containing a solution with 50:50 water:antifreeze (Prestone LowTox, Old Ridgebury, Connecticut, USA). This antifreeze with propylene glycol as active ingredient was employed due to its low toxicity. Traps were placed with their rims flush with the surrounding soil and were collected after 5 d. Pitfall trapping is an effective and commonly employed method for sampling ant communities (Bestelmeyer et al. 2000). In our resurvey, we conducted all sampling between May and July 2017 (the same seasonal interval as in the original survey). We deployed a total of 935 pitfall traps (187 arrays). After traps were removed from the field, we counted and identified all individual arthropods. Ants were identified to genus using Fisher and Cover (2007), and to species using AntWeb (2018). A reference collection of ants from 1996 is deposited at the Bohart Museum of Entomology at UC Davis (original survey), and in the Suarez Lab at the University of Illinois at Urbana-Champaign (current survey). Only workers of aboveground foraging ant species were included in the statistical analyses as hypogeic ants in these habitats are not adequately sampled with just pitfall traps (as in Suarez et al. 1998).

Statistical analyses

All analyses were conducted in R 3.5.0 (R Development Core Team 2018), and figures were produced with ggplot2 version 3.1.0 (Wickham et al. 2018). To examine how the effects of habitat loss, fragmentation and the impacts of *L. humile* invasion might have changed over time, we analyzed data both at the level of the fragment and at the level of individual arrays, with the objective

of identifying differential responses to native ants that may be occurring on a local scale (arrays) as well as the landscape level (fragments).

We performed two analyses at the fragment level. First, we used generalized linear models (GLMs) with Poisson responses (log-link function) to assess how native ant species richness varied with fragment-level descriptors (using R package MASS, version 7.3-5.1; Ripley et al. 2018). These analyses emulated those used in Suarez et al. (1998), where each fragment represented a sampling unit for analysis, and included the following predictor variables: (1) fragment area, (2) time since isolation, (3) degree of isolation, (4) irregularity of the perimeter, and (5) mean Argentine ant abundance. Mean abundance for *L. humile* was estimated for each fragment by first calculating the average number of workers per jar at each array, then averaging the number of Argentine ant workers per array for a single value for the fragment. The total area of each fragment was \log_{10} -transformed due to the distribution of values between the smallest and largest fragments. No overdispersion was detected and Bayesian information criteria (BIC) was used for model selection (Aho et al. 2014). The significance of the variables in the final model was evaluated with a likelihood ratio test (Beckerman et al. 2017). Despite a positive correlation between time since isolation and degree of isolation ($\rho = 0.68$, $P < 0.05$), all variance inflation factors (VIF) are lower than 2.7. Thus, potential problems related to multicollinearity (James et al. 2014) are expected to be minor among the five predictor variables considered (Appendix S1: Fig. S2).

The second fragment-level analysis tested for changes in the species–area relationship between sampling years (1996 vs. 2017), and between fragments and plots from the unfragmented control area in 2017 (Elliott Chaparral Reserve). We employed GLMs to compare the slopes and intercepts of the species–area relationship (Crawley 2012). For these analyses, we used the count data on richness of native species as a response variable, and the log area (continuous) and year (categorical) as explanatory variables. This model was run with Poisson error structure and the log-link function, and there was no evidence of overdispersion (residual deviance: 95.98, $df = 84$).

For the array-level analyses, a generalized linear mixed model (GLMM) (R package lme4, Version 1.1-19; Bates et al. 2018) was used to test whether the richness of native ants per array depended on the mean Argentine ant abundance, and if this relationship changed between sampling periods (categories: 1996 and 2017). “Fragment” was included in the model as a random effect to account for potential correlation among arrays within the same fragment. For this model we used a Poisson distribution and a log-link function. Arrays within the Elliott Chaparral Reserve (unfragmented control site) were included in this comparison. As an alternative response variable, we also calculated the proportion of traps in each array that captured Argentine ants. The

two estimates of abundance were significantly correlated ($\rho = 0.32$; $P = 0.03$), and results are presented as a more conservative estimate of Argentine ant abundance compared to mean of worker counts (Appendix S1: Fig. S3).

We used the distance of each sample array to the nearest urban edge to evaluate if Argentine ant mean abundance and native ant species richness varied in relation to the effects of habitat fragmentation per se (Fahrig 2003, 2017). In both analyses, we included two categorical variables: distance of the array to the nearest urban edge (five categories of distances: 0–25, 25–50, 50–100, 100–200 and >200 m), year (1996 and 2017), and their interactions as independent variables, with Argentine ant mean abundance and native ant species richness as response variables. We performed analyses of deviance using count data with (1) Gaussian distribution and the link identity for Argentine ant mean abundance and (2) negative binomial distribution with log-link function for native ant richness (R package MASS, version 7.3-5.1; Ripley et al. 2018). We evaluated the probability distribution that best fit our data using the function `qqf` from the R package `car` (Version 3.0-6; Fox and Weisberg 2019), and multiple comparisons among categories of distance per year were made with the package `lsmeans` (Version 2.30-0; Russell 2018). These approaches are consistent with Suarez et al. (1998).

We also examined how the species–area relationship changes for the 40 fragments when taking into account different distances from the edge where Argentine ants are most abundant. Native ant species was used as response variable, and three values of fragment area were calculated for the explanatory variables: the total area of the fragment, the area greater than 100 m from an edge, and the area greater than 200 m from an edge. This GLM was run with Poisson error structure and the log-link function.

To investigate if Argentine ant mean abundance among fragments has changed in the last two decades, we used a paired Wilcoxon signed rank test between 1996 and 2017 (Crawley 2012). For this test, we used data on the Argentine ant mean abundance for both years to run the analysis. We also examined whether the overall number of arrays with Argentine ants has changed, a surrogate for overall invaded area, with a two-way analysis of deviance (Crawley 2012). The response variable was the proportion of traps per array in which the Argentine ant was present with two categorical variables and their interaction as responses: year (1996 and 2017) and fragment. Due to an over-dispersed model during the exploratory analyses, we used quasi-binomial errors and the logit function in the model. The same analysis but with count data was used to examine changes in the richness of native species (response variable) between periods of sampling and the interaction with the fragments evaluated. This model was fit using Poisson errors and the log-link function.

We took advantage of additional temporal sampling at one fragment to document how changes in Argentine

ant mean abundance and native ant richness have changed over time. Rice Canyon (78.19 ha) was isolated from continuous scrub habitat by urbanization in 1993, and we sampled nine arrays at this site in each of eight years (1996–1998, 2000–2003, and 2017; Appendix S1: Fig. S1b). We used GLMs (deviance analyses) to test if richness of native ant species and the mean abundance of *L. humile* changed among sampling periods in the Rice Canyon fragment. Due to overdispersion in both models (native ants: residual deviance, $rd = 128.4$, $df = 64$; and abundance of *L. humile*: $rd = 12,999$, $df = 64$), we ran these analyses with quasi-Poisson error structure and the log-link function. Multiple comparisons were used to test if the mean abundance of Argentine ant and richness of native species differed among years (R package `lsmeans`). Finally, we estimated the effect size (sensu Cohen 1988) for the differences in Argentine ant prevalence and native ant richness across the 40 fragments between the two sampling periods (Crawley 2012).

RESULTS

In 2017, we collected a total of 42,002 ant workers belonging to 28 aboveground foraging species (32 total native species) and five introduced species (Appendix S1: Table S2). Pitfall traps located in unfragmented plots within the Elliott reserve, where 9,705 of these workers were collected, did not capture any introduced species. Argentine ant relative abundance in the fragments was higher in 2017 compared to 1996. In 2017, *L. humile* made up 91% (29,266 out of 32,297) of all ant workers captured, whereas in 1996, *L. humile* represented 41% (9,113 out of 22,070) of all captures. The number of native ant workers captured in 2017 was only 23% of that from 1996 (3,031 vs. 12,957), despite the same sampling effort. Importantly, environmental conditions during summers 1996 and 2017 did not differ in the amount of rain (Wilcoxon; $W = 13.5$, $P = 0.91$) or in the air temperature ($t_{(8)} = -0.16$; $P = 0.87$; Appendix S1: Fig. S4).

At the fragment level, area was the only significant predictor of native ant richness in 2017 ($\chi^2 = 23.22$, $df = 1$, $P < 0.001$). In contrast, in 1996 three descriptors predicted the fragment-level richness of native ant species: area (+) ($\chi^2 = 46.39$, $df = 1$, $P < 0.001$), time since isolation (–) ($\chi^2 = 6.47$, $df = 1$, $P = 0.01$), and mean abundance of Argentine ant (–) ($\chi^2 = 3.75$, $df = 1$, $P = 0.05$) (Table 1). When we compared the species–area relationships among plots within the control area and the fragments (Fig. 2), both the intercept and the slope were significantly lower for the fragment data set than for the plots in control area (intercept $z = 4.74$, $P < 0.001$; slope $z = -2.35$, $P = 0.02$). However, there was no difference in the slope or the intercept of the species–area relationship between the fragment data sets from 1996 and 2017 (intercept $z = 1.14$, $P = 0.25$; slope $z = -1.34$, $P = 0.18$; estimates for intercepts and slopes are given in the legend of Fig. 2).

TABLE 1. Fragment-level predictors of the number of aboveground foraging native ant species among fragments sampled in 2017 and 1996.

Variable	Estimate	SE	z	P
2017				
Intercept	0.1148	0.2497	0.460	0.646
log(area of the fragment)	0.8559	0.1807	4.737	<0.0001
1996				
Intercept	0.28986	0.32339	0.896	0.3701
log(area of the fragment)	1.04365	0.18081	5.722	<0.0001
Time since isolation	-0.01071	0.00437	-2.450	0.0143
Mean Argentine ant abundance	-0.00076	0.00123	-0.622	0.0528

Note: Statistical results are from GLM's where the most parsimonious model was selected using Bayesian information criterion (BIC = 152.21).

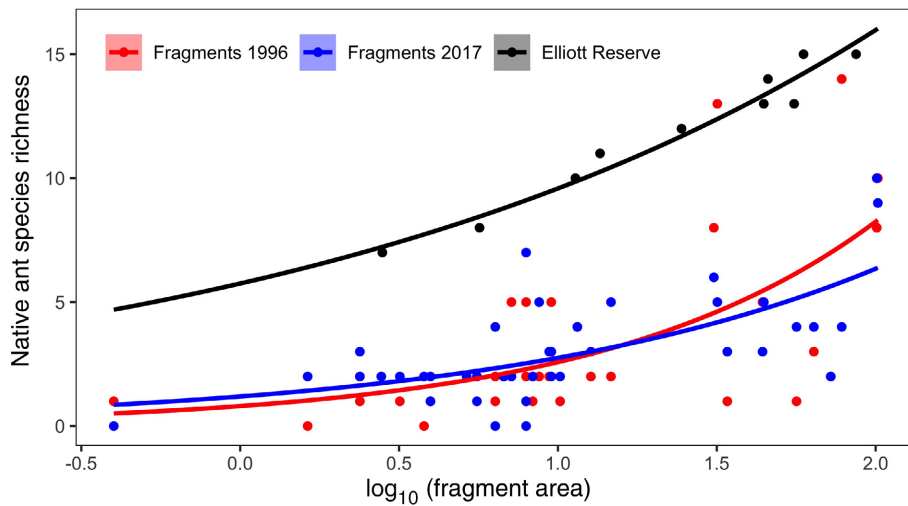


FIG. 2. Species–area relationships for fragments and similarly sized plots within continuous habitat (Elliott) in 1996 and 2017. Fragment area was measured in hectares. Estimates for plots within Elliott reserve (mean \pm SE): intercept = 1.749 ± 0.41 ; slope = 0.511 ± 0.27 . Estimates for fragments 1996: intercept = -0.215 ± 0.25 ; slope = 1.162 ± 0.17 . Estimates for fragments 2017: intercept = 0.177 ± 0.34 ; slope = 0.835 ± 0.24 .

At the level of individual trap arrays, the number of native ant species at the array declined with the mean abundance of Argentine ants per array in both 1996 and 2017 ($\chi^2 = 6.78$, $df = 1$, $P = 0.01$; Fig. 3). However, in 2017, arrays with no Argentine ants had fewer native ant species than did arrays with no Argentine ants in 1996 (intercept $\chi^2 = 4.22$, $df = 1$, $P = 0.04$; Fig. 3). On the other hand, the proportion of arrays that were completely occupied by Argentine ants increased between the sample periods. In 1996, 55% of the arrays had Argentine ants in all five traps, while in 2017 this percentage increased to 75% ($\chi^2 = 14.94$, $df = 1$, $P < 0.001$).

The relationship between Argentine ant mean abundance at an array and distance of the array to the nearest urban edge also differed between 2017 and 1996 (year $F_{1,8} = 44.51$, $P < 0.001$; year \times distance to urban edge interaction $F_{4,8} = 5.19$, $P < 0.001$; Fig. 4a). In addition to observing higher mean Argentine ant abundance in

2017 compared to 1996, arrays between 100–200 m from an urban edge had higher *L. humile* abundance in 2017 compared with 1996 ($z = 5.083$, $P < 0.001$; Fig. 4a). In the original study, Argentine ants were uncommon in arrays greater than 100 m away from the urban edge, but in 2017, only arrays located farther than 200 m from an urban edge showed reduced Argentine ant activity. Conversely, the richness of native ant species at any array in 1996 was positively correlated with the distance to the nearest urban edge. Arrays located between 50 and 100 m and arrays farther than 100 m from the urban edge had a higher number of native ant species in 1996, compared to 2017 (50–100 m $z = 2.82$, $P = 0.004$; 100–200 m $z = 5.078$, $P < 0.0001$; Fig. 4b).

These edge effects had fragment-wide consequences (Fig. 5). The larger the internal area of a fragment, either greater than 100 m or 200 m from an edge, the higher the number of native ant species remaining in the fragment (GLM $\chi^2 = 29.45$, $df = 2$, $P < 0.0001$). On

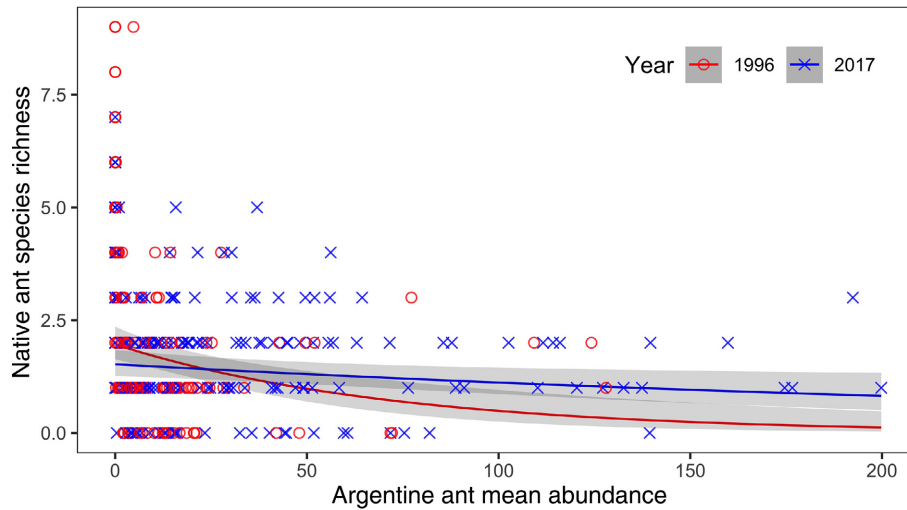


FIG. 3. Relationship between the number of native ant species detected at a sampling array and the mean number of Argentine ants at that array in 1996 ($y = e^{0.673294 - 0.013892x}$) and in 2017 ($y = e^{0.420073 - 0.003094x}$).

average, more species of native ants were found in 1996 than in 2017 (negative binomial $P < 0.001$; year \times distance to urban edge interaction $P < 0.001$; Fig. 4b).

We found evidence for an increase among fragments in the mean abundance of Argentine ants over the past two decades ($V = 174$, $P = 0.001$; Appendix S1: Fig. S5). In addition, the proportion of traps per array with Argentine ants, a surrogate for overall invaded area, increased between surveys in seven out of 40 habitat fragments (GLM $F_{1,38} = 3.93$, $P = 0.001$) and exhibited no change in the remaining fragments (Appendix S1: Table S3). The seven fragments in which the Argentine ant expanded its range are among the largest surveyed (>30 ha) and in 1996, had relatively low occupancy of *L. humile*. Fragment-level changes in native ant species richness also exhibited a significant year and fragment interaction ($\chi^2 = 171.93$, $df = 38$, $P < 0.0001$). Only the two fragments that had the highest native ant richness and were recently (3 yr) isolated in 1996 showed a significant ($> 60\%$) decline in the number of native ant species: Rice Canyon ($z = 4.28$, $P < 0.0001$) and Home Depot Canyon ($z = 4.67$, $P < 0.0001$).

Within fragments, three native aboveground species (*Cyphomyrmex wheeleri*, *Monomorium ergatogyna*, and *Tetramorium spinosum*) and two introduced species (*Brachymyrmex patagonicus* and *Pheidole flavens*) detected in 2017 were absent from summer surveys in 1996. *Brachymyrmex patagonicus* and *P. flavens* were not detected during ant survey period 21 yr ago, but two of the native species (*C. wheeleri* and *T. spinosum*) were detected in the fragments in additional winter samples in 1996. In contrast, seven native species detected in 1996 were missing from the 2017 survey: *Neivamyrmex californicus*, *Dorymyrmex bicolor*, *Camponotus dumetorum*, *Camponotus vicinus*, *Formica moki*, *Temnothorax nevadensis*,

and *Pheidole hyatti* (Appendix S1: Table S2). Each of these species was detected in three or fewer fragments in 1996. *Neivamyrmex* and *D. bicolor* were found only in two to three large fragments in 1996, including Rice Canyon and Home Depot Canyon. *Camponotus dumetorum*, *C. vicinus*, and *F. moki* were lost from the only fragment where they occurred in 1996 (Acuna). Notably, *D. bicolor* and *P. hyatti* both appeared relatively abundant where they occurred in 1996.

The Rice Canyon site provides more complete temporal sampling and further reveals how invader impacts change over time. At this site, native ant species richness declined over the 21-yr sampling period ($F_{1,7} = 7.27$, $P < 0.001$; Fig. 6a). Declines in native ant richness over time were contemporaneous with increases in Argentine ant mean abundance ($F_{1,7} = 4.68$, $P < 0.001$; Fig. 6b).

Summarizing the information gathered across the 40 fragments between 1996 and 2017, the largest positive effect size was for the proportion of traps in which Argentine ants were detected ($d = 0.603 \pm 0.16$; mean \pm SE), followed by Argentine ant mean abundance ($r = 0.379 \pm 0.09$). In contrast, effect size for the number of native ants ($r = -0.021$; ± 0.11) and proportion of traps with native ant workers ($d = -0.204 \pm 0.11$) were negative (Appendix S1: Fig. S6).

DISCUSSION

Habitat loss and degradation can interact with biological invasions to provide a deterministic mechanism for reduced biodiversity (Hobbs and Huenneke 1992, Ewers and Didham 2006, King and Tschinkel 2008). We resurveyed 40 fragments of scrub habitat that varied in degree of invasion to determine (1) if the same fragment-level variables predict native ant species

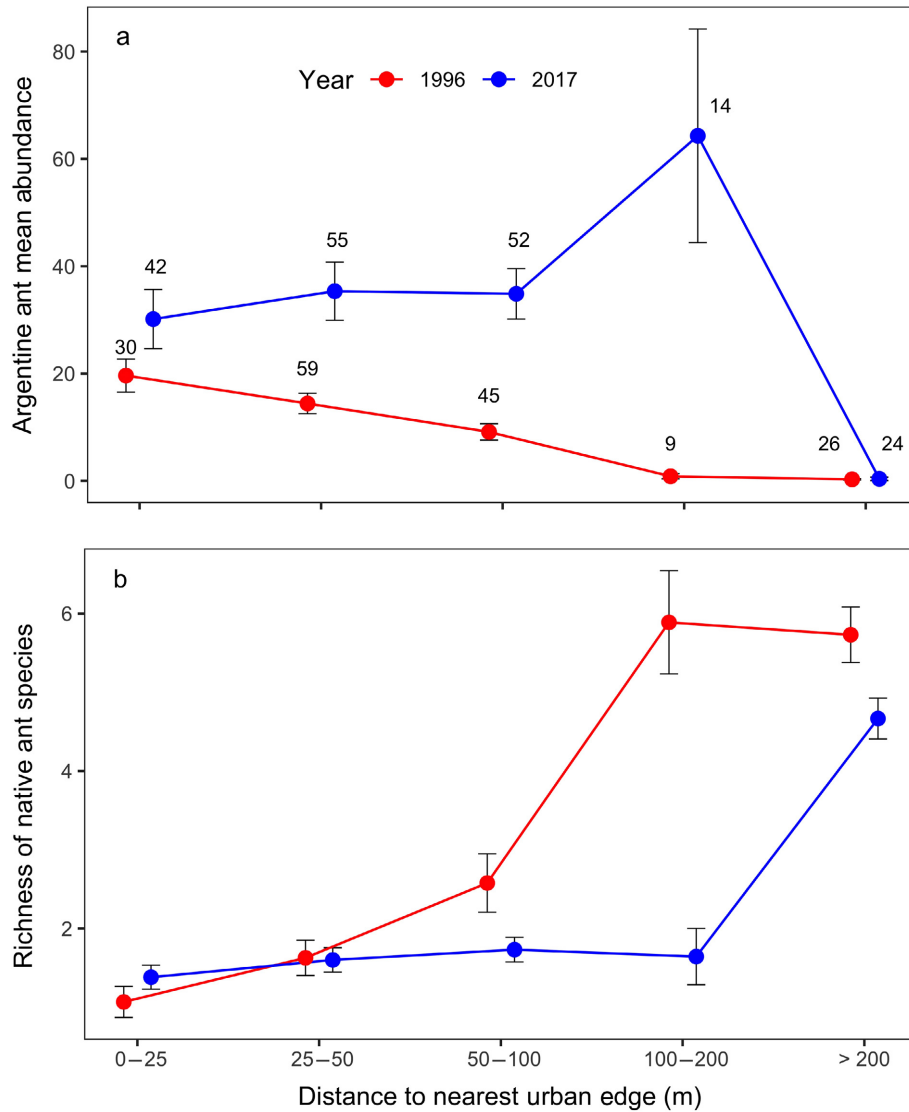


FIG. 4. (a) Argentine ant mean abundance (i.e., average number of workers per jar per sample array) and (b) the number of native ants detected at sample arrays vs. the distance of the array to the nearest urban edge. The numbers above the points indicate the number of arrays (sample size) for each category of distance. Error bars represent \pm SE.

richness at each site as 21 yr ago, (2) how the distribution and relative abundance of Argentine ants changed over time, and (3) if native ants show signs of recovery or further decline as predicted by Suarez et al. (1998). Fragment size was the only remaining predictor of native ant richness in the fragment-level analysis of the 2017 resurvey data. At the level of individual arrays, the distribution and mean abundance of Argentine ants increased in 2017 relative to 1996. Finally, native ants did not show signs of recovery; we detected fewer species and a lower proportion of traps with native ant workers relative to that found 21 yr ago. Our results support that the effects of invasive species can be pervasive in fragmented landscapes.

Most of our sites consist of steep slopes and valleys that are unsuitable for further urban development. Therefore, fragment area did not change substantially over the last 21 yr, and this variable remained the best predictor of native ant richness at the landscape level. In contrast, fragment age (e.g., the number of years since their isolation from continuous habitat) no longer predicted native ant richness. In 1996, there were seven fragments that had been isolated for less than 10 yr at the time of the survey. These seven fragments had the highest ant diversity in 1996, and it was at these sites where the most native ants were lost in the present resurvey. In the current survey, fragment age has increased by 21 yr, and no fragments have been isolated for less than 24 yr,

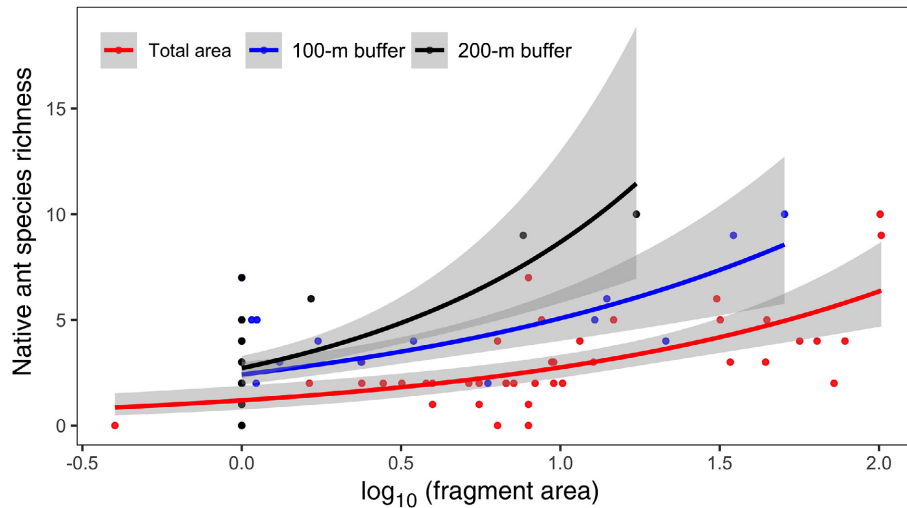


FIG. 5. Comparison of the species–area relationship for the number of native ant species within fragments depending on their internal area. There is no evidence of overdispersion (residual deviance = 112.76 on 116 df). Fragment area was measured in hectares.

which appears to be enough time for Argentine ants to have exerted their impact on native ants. The degree of isolation of individual fragments from larger expanses of habitat (e.g., potential sources) was not significantly related to native ant richness in either time period, consistent with other fragmented systems (Watling and Donnelly 2006). Argentine ant mean abundance was negatively correlated with native ant richness in 1996, but this variable no longer predicted native ant richness at the fragment scale in 2017. This change may be a consequence of the increased occupancy of Argentine ants in traps; few fragments had Argentine ant-free refugia for native ants by 2017. This pattern was particularly prominent in two young fragments (Rice Canyon and Home Depot) that had few Argentine ants and high species richness in 1996 yet few native ants and 100% occupancy of Argentine ants in 2017. Two fragments retained relatively high native ant diversity: Chula Vista Edge and Kate Sessions. This finding likely reflects the higher topography of these sites, which does not concentrate urban water runoff. Argentine ants avoid chronically dry conditions (Holway et al. 2002b, Menke et al. 2007), suggesting that native ant diversity can be retained in fragments with features that promote aridity even 46 yr after isolation (in the case of Kate Sessions).

Edge effects in fragmented landscapes can strongly influence local abiotic conditions (Ries et al. 2004). In southern California, for example, urbanization promotes conditions that increase the invasion of Argentine ants into natural areas (e.g., increased moisture availability; Holway et al. 2002b, Holway and Suarez 2006, Bolger 2007) that in turn reduce native ant species richness. In 1996 the Argentine ant was most abundant near urban edges, and its ability to penetrate into fragments was restricted at distances around 100 m from an edge. Subsequently, Suarez et al. (1998) estimated that in coastal

southern California a distance of 200 m from an urban edge would be necessary to maintain populations of native ants. However, we found Argentine ant abundance highest between 100 and 200 m from an edge, and even 200 m away from an urban edge may be insufficient to preserve native ant diversity in some areas, indicating that edges have large and clear negative effects for native ants, especially in conditions where fragmentation and biological invasion are prevalent. It is worth noting that our survey in 2017 followed a relatively wet winter for southern California, and these conditions may have allowed the Argentine ant to increase in abundance away from fragment edges (Holway and Suarez 2006, Heller et al. 2008).

At the scale of individual arrays, we saw a reduction in native ant richness (relative to the results of the original survey), even at sites with few or no Argentine ants. This finding may reflect extirpation and a lack of recruitment at the fragment level due to declines in native ant abundance in surrounding areas. This pattern may be particularly common in habitat remnants and might be related to an extinction debt where eventual biodiversity loss is inevitable despite the relatively long-term persistence of species after fragmentation (Kuussaari et al. 2009). This pattern may also be caused by the “ghost of invasion past” (Reynolds et al. 2017): the Argentine ant may move into areas, displace native ants, and then move out of the area as abiotic conditions change (e.g., soil moisture decreases) or resource availability shifts (e.g., Markin 1970). Despite that over the last 21 yr native ants continued to be lost at these local scales (i.e., 20-m² sampling area of an array), this loss of species has yet to alter the species–area relationship at the landscape level.

Finer-scale temporal sampling at Rice Canyon provides evidence for chronological displacement, reduced

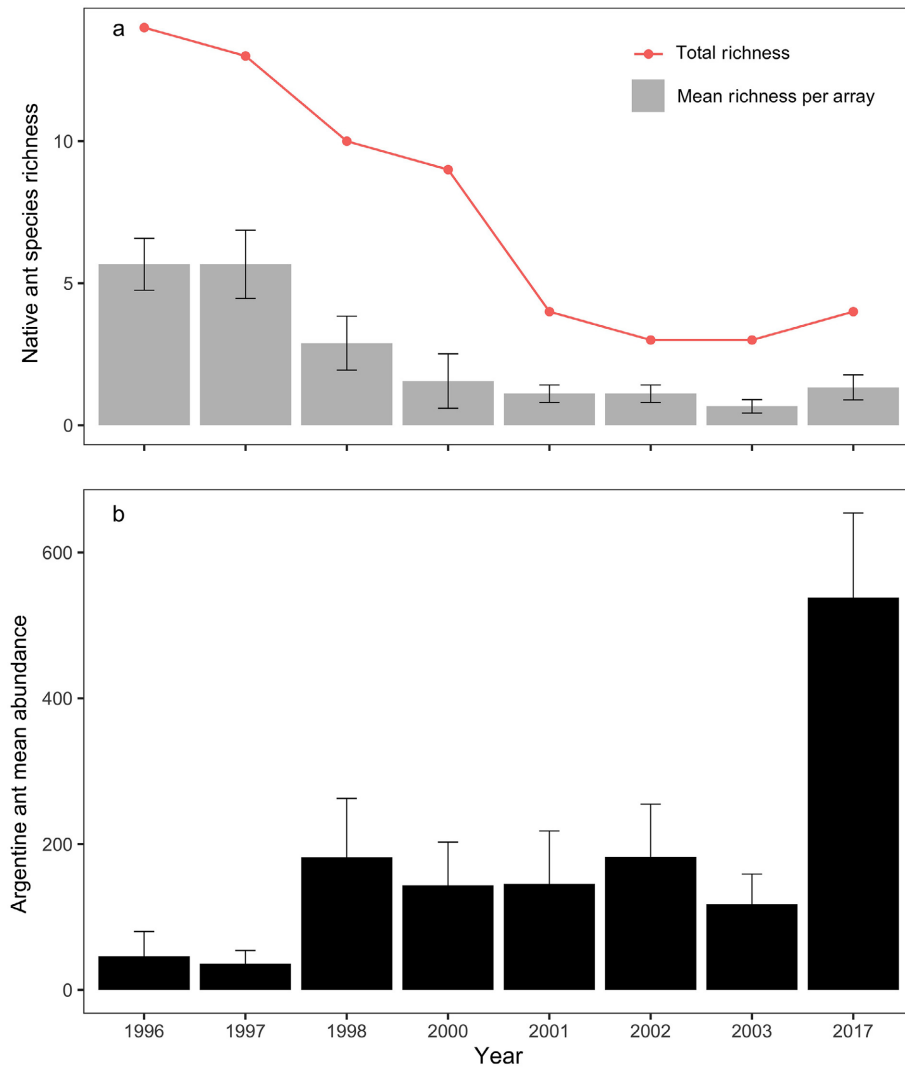


FIG. 6. Times series of native ant richness and Argentine ant mean abundance (i.e., average number of workers per jar per sample array) over eight annual sample periods between 1996 and 2017 at Rice Canyon, San Diego County, California, USA. (a) Number of native ant species for the entire fragment (red line) and mean number of native ant species per array (bar graphs) through time. (b) Changes in the mean abundance of Argentine ants through time. Bars represent mean and SE.

richness of native species, and the relative stability (or apparent increase) in the mean abundance of *L. humile* through time. This site, which was isolated from continuous habitat three years before 1996, harbored more than 21 native ant species, 14 of which were detected in summer pitfall sampling in 1996 (Suarez et al. 1998). Of these 14, 10 were absent from our 2017 sampling, including the army ant *Neivamyrmex californicus*. This species almost exclusively preys upon ant broods by raiding colonies of *Veromessor andrei*, *Pheidole californica*, and *Pheidole hyatti* (Droual and Topoff 1981, Ward 1999). *Pheidole hyatti* was common in Rice Canyon in 1996 but completely absent in our recent resurvey. Other species reduced or missing from our 2017 sampling include harvester ants (*Veromessor*) and carpenter ants

(*Camponotus*), which, along with army ants, were identified as among the most vulnerable species 21 yr ago (Suarez et al. 1998). For example, *Camponotus dumetorum*, a species with an extremely low occurrence in 1996 and absent in 2017, is restricted to the California floristic province and its foraging activity is completely reduced in invaded areas by *L. humile* (Ludka et al. 2015). Other resurvey data from California have also found these native ant taxa to be negatively associated with sites occupied by the Argentine ant (Menke et al. 2018, Naughton et al. 2020).

The long-term population dynamics and impacts of invasive species are difficult to predict, irrespective of taxon. Not only are long-term studies needed, but generalizations remain difficult given what we know from case

studies. For example, invasive plants such as garlic mustard (*Alliaria petiolata*) or giant hogweed (*Heracleum mantegazzianum*) have acute detrimental effects on native species, but invaded communities may recover over time (Lankau et al. 2009, Dostal et al. 2013). In contrast, pervasive chronic effects occur in ecosystems invaded by the peacock bass (*Cichla monoculus*) in Panama up to 45 yr after its introduction (Sharpe et al. 2017). A diversity of studies on plant invasion has shown that while impacts might change over time (Lankau et al. 2009, Flory et al. 2017), mainly due to biotic and abiotic features of the invaded ecosystem (Diez et al. 2010, Flory and Clay 2013), a fundamental aspect to understand whether the impacts will change relates to the invader abundance (Parker et al. 1999). Thus, ecosystems that have been exposed for long periods of time to high invader abundance in the long term showed disruption of ecosystem processes and lower biotic resistance even after decline in the population of invaders (Grove et al. 2017, D'Antonio et al. 2017).

Ant invasions also exhibit diverse trajectories with apparent population declines reported for the red imported fire ant (Morrison 2002), Argentine ant (Cooling et al. 2012), and the yellow crazy ant (Cooling and Hoffman 2015). Furthermore, there is some evidence that native ant assemblages can recover following these collapses (e.g., fire ants at Brackenridge Field Laboratory, Texas; Porter and Savignano 1990, Morrison 2002). In contrast, a recent reexamination of 20 riparian woodland sites in northern California over a 30-yr period indicates that the effects of the Argentine ant can endure over decadal time scales (Menke et al. 2018). Moreover, recent resurvey data from urban sites in San Diego County also revealed regional-scale Argentine ant persistence (Menke and Holway 2020). However, most long-term studies on ant invasions (including this one) are restricted to few time points and therefore miss year-to-year variation in population dynamics that may provide insight into mechanisms responsible for how native species respond to invasion. For example, yearly sampling of Argentine ant occupancy from 1993 to 1999 at Jasper Ridge reserve in Northern California showed that this species increased its range size at a rate of 5 ha/yr (Sanders et al. 2001). Given the role of abundance on impact and overall pattern of invasion (Parker et al. 1999, Lankau et al. 2009, Strayer et al. 2011, Ricciardi et al. 2013), developing a time series of invader abundance to test for density dependent impacts should be a priority for future research (Naughton et al. 2020).

Although detailed chronological histories of ant invasion are uncommon, our results provide evidence that invaders can maintain high numerical dominance over long periods of time. Despite the difficulties in making the study of biological invasion a more predictive science (e.g., effects of invasions being scale dependent: this study and also see Davies et al. 2005), studying the associations between invasions and other controlling factors (e.g., environmental disturbance, physical conditions)

will also aid in understanding the worst ecological effects of widespread invaders, such as the regional extirpation of native species. Ants are identified as ecosystem engineers (Folgarait 1998), and we still do not know if the Argentine ant has modified the environment in ways that could promote its long-term impacts (e.g., Reynolds et al. 2017) or facilitate the introduction of additional nonnatives (Simberloff and Von Holle 1999, Helms and Vinson 2002). For example, in the study area we detected two introduced species, *B. patagonicus* and *P. flavens*, both of which have been spreading throughout the southwestern U.S. over the last two decades. Moreover, recent sampling in urban sites in San Diego County revealed the presence of the big-headed ant (*Pheidole megacephala*; Menke and Holway 2020). Additional research is needed to determine how communities made up of multiple introduced species arise and are maintained in these environments.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecsy.3257/supinfo>

DATA AVAILABILITY

Data are available in Figshare: <https://doi.org/10.6084/m9.figshare.13264901.v1>.