

## Multiyear drought exacerbates long-term effects of climate on an invasive ant species

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**Abstract.** Invasive species threaten biodiversity, ecosystem function, and human health, but the long-term drivers of invasion dynamics remain poorly understood. We use data from a 28-yr ongoing survey of a Northern California ant community invaded by the Argentine ant (*Linepithema humile*) to investigate the influence of abiotic and biotic factors on invasion dynamics. We found that the distribution of *L. humile* retracted following an extreme drought that occurred in the region from 2012 to 2015. The distribution of several native ant species also contracted, but overall native ant diversity was higher after the drought and for some native ant species, distributions expanded over the 28-yr survey period. Using structural equation models, we found the strongest impact on the distribution of *L. humile* was from direct effects of climate, namely, cumulative precipitation and summer maximum temperatures, with only a negligible role for biotic resistance and indirect effects of climate mediated by native ants. The increasing drought and high temperature extremes projected for northern California because of anthropogenic-driven climate change may limit the spread, and possibly the impact, of *L. humile* in invaded regions. The outcome will depend on the response of native ant communities to these climatic stressors.

*Key words:* Argentine ant; drought; invasion; structural equation modeling.

### INTRODUCTION

Because biological invasions threaten global biodiversity, ecosystem function, and human health, a major goal of conservation biology and ecological research is to predict the establishment and spread of invasive species (Vilà and Hulme 2017). Climatic suitability is often a key factor in invasion success at both landscape and global scales, leading climate change to alter the establishment and spread of invasive species (Hellmann et al. 2008, Roura-Pascual et al. 2011). However, it remains challenging to predict the impact of future climate change on invasion success as long-term data sets on biological invasions in natural settings are rare (Strayer et al. 2017). In this study, we draw on one of the most complete, long-term data sets of an ongoing biological invasion during a once-in-a-millennium drought event to investigate the direct and indirect effects of climate on

the dynamics of an Argentine ant invasion in Northern California.

Native to South America, the Argentine ant, *Linepithema humile*, is a widespread and ecologically destructive invasive species (Holway et al. 2002a, Roura-Pascual et al. 2011, Menke et al. 2018, Lowe et al. 2010). Facilitated by human-mediated dispersal, *L. humile* has become established on six continents and many oceanic islands. Initially detected in California around 1905 (Smith 1936), it is now widespread across much of the state, but limited in xeric environments and at high elevations. Throughout its introduced range, *L. humile* has displaced native ant species (Holway et al. 2002a), reduced the diversity of other arthropod species (Human and Gordon 1997), induced shifts in native ant community structure (Sanders et al. 2003, Achury et al. 2021), and disrupted ecosystem processes through trophic cascades (Bond and Slingsby 1984, Gómez et al. 2003).

At both global and local scales, the distribution of *L. humile* is associated with climatic suitability, human land modification and, to a lesser extent, biotic resistance by native species (Krushelnicky et al. 2005, Menke and

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Holway 2006, Menke et al. 2007, Roura-Pascual et al. 2011). In northern California, proximity to human development, soil moisture, and interactions with the native winter ant, *Prenolepis imparis*, are the main predictors of the local distribution of *L. humile* (Fitzgerald et al. 2012, Fitzgerald and Gordon 2012, Gordon and Heller 2014, Menke et al. 2018). In this region, temporal fluctuations in *L. humile* abundance and spread are strongly associated with seasonal and annual variation in precipitation and native ant presence (DiGirolamo and Fox 2006, Heller and Gordon 2006, Heller et al. 2008, Fitzgerald and Gordon 2012). Most of these prior studies investigated the spread of *L. humile* as its range continued to expand. However, in some regions, studies have found that the local distribution of *L. humile* has contracted in recent decades (Wetterer et al. 2006, Cooling et al. 2012).

We use a 28-yr, ongoing survey of the ants at Jasper Ridge Biological Preserve (JRBP), a 483-hectare reserve in northern California, to investigate the influence of abiotic and biotic factors on the distribution of *L. humile*. Ant surveys have been conducted biannually at JRBP since 1993 (Human et al. 1998, Ingram and Gordon 2003). Over the next 8 yr, *L. humile* spread from the periphery of the reserve towards the interior in seasonal pulses, as the invasion front advanced in the summer and contracted in the winter, until it reached a stable invasive range around 2001 (Heller et al. 2008, Fitzgerald and Gordon 2012). However, the region experienced record-breaking drought beginning in the winter of 2011, peaking from 2012 to 2015, during which time the cumulative rainfall deficit was estimated to be unprecedented in the last 1,200 yr (Asner et al. 2016). This offered an opportunity to assess the impact of extreme climatic events on invasion dynamics.

We bring together this unique long-term data set and climatic event to ask (1) How have the distributions of *L. humile* and native ant species changed over the 28-yr survey period? (2) How were the distributions of *L. humile* and native ant species affected by the 2012–2015 drought? (3) How has climate, directly and indirectly, via its effect on native ant species, shaped the distribution of *L. humile*?

## METHODS

### *Study site and data collection*

All surveys were conducted at Jasper Ridge Biological Preserve (JRBP), a 483-hectare preserve in the eastern foothills of the Santa Cruz mountains in San Mateo County, California, United States (37°24' N, 122°13'30' W; 66–207 m; Appendix S1: Fig. S1). Surveys were conducted twice annually, once in May (spring surveys) at the end of the winter rainy season, and once in September (fall surveys) at the end of the dry summer season. Survey sites are in the center of each 1-ha quadrat in the preserve (Heller 2005). On average, 288 ( $\pm 41$ ) sites were surveyed each May and September. Some sites were surveyed only intermittently because of dense poison oak

or flooding. We confine our analyses to the plots that were surveyed every year, or every year except one, between May 1993 and May 2020 ( $n = 226$  plots). The survey data record the presence of ant species at a site. At each site, a circle of 20-m radius was visually searched for five person-minutes, and the presence of native ant species and *L. humile* was recorded (Appendix S1: Section S1). Native ants were identified to species or genus in all surveys except in May and September 1993 and May 1996, so data from these three surveys were removed from the analysis of ant distributions and native ant richness and diversity. We use the term “distribution” to describe the spatial extent in sites occupied by a particular ant species during the survey. However, whether a species is seen at a site is likely influenced by seasonal differences in activity and detectability.

Over the course of the surveys, 31 ant species have been documented at JRBP (Heller et al. 2008), 13 of which were detected in many or all years of the biannual surveys (see Appendix S1: Table S1). For this analysis we focus on *L. humile* and the five most common native ant species: *P. imparis*, *Camponotus* spp. (typically either *C. semitestaceus* and *C. laevigatus*, which are impossible to distinguish in the field), *Formica* spp. (typically *Formica moki* or *Formica subpolita*, which were not consistently distinguished during the survey), *Messor andrei*, and *Tapinoma sessile*.

Daily data on precipitation were obtained from the JRBP weather station (37°23'12' N, 122°14'26' W).

### *Changes in the distribution of L. humile and native ant species over the survey period*

We analyzed trends in ant distributions as the number of survey sites occupied by a given species. Because there is species-specific, seasonal variation in ant activity (Heller et al. 2008), we analyzed data from spring and fall surveys separately (Appendix S1: Section S1). For each species, we compared the number of hectares occupied in fall and spring using Mann–Whitney U-tests. We examined yearly variation in ant species distributions from 1993 to 2020 using a modified Mann–Kendall trend test, which corrects for serial autocorrelation in trend analysis. We also analyzed temporal trends in native ant species richness and evenness at the preserve level using the *vegan* and *benthos* package in R v 4.0.2 (Dixon 2003). We used Hurlbert’s probability of interspecific encounter (PIE), the probability that two individuals selected at random from a sample belong to different species, as an evenness metric. We repeated the richness and diversity analyses after removing species that were rarely observed (<20 times over the survey period; Appendix S1: Table S1, Fig. S6).

### *Effect of drought on L. humile and native ant distributions*

We compared the distributions of *L. humile* and native ant species, native ant species richness, and

evenness (PIE) before, during, and after the 2012–2015 drought. We used pairwise Wilcoxon tests, a nonparametric test that corrects for multiple testing, and ran separate tests for fall and spring distributions.

#### *Direct and indirect effects of climate on L. humile distribution*

We used structural equation modeling (SEM) to test for direct and indirect effects of climate, mediated through changes in native ant communities (Grace et al. 2010). Using a priori knowledge from extensive previous work in JRBP, we constructed a meta-model relating the distribution of *L. humile* and of five native ant species, and climate (Appendix S1: Section S1, Fig. S2). In the model, climate directly affects *L. humile*, *P. imparis*, and native ant distributions. Climate variables included 4-yr cumulative precipitation preceding the survey, winter minimum temperature, and summer maximum temperature. Because spring surveys occur before the same-year summer conditions, prior-year summer maximum temperature was included as a potential predictor of spring ant distributions. Any variables not meeting the assumptions of homogeneity of variances or normality (i.e., prior summer maximum temperature) were log-transformed. We fit the full model, including all causal links through maximum-likelihood estimation with robust standard errors using the *lavaan* package in R v 4.0.2 (Rosseel 2012). As the full model fit the data poorly ( $\chi^2 = 33.04$ ,  $P = 0.007$ ,  $cfi = 0.588$ ), we then iteratively removed paths with weak statistical support ( $P > 0.2$ ) until the model no longer improved significantly (Grace et al. 2010). To test for indirect effects of climate on *L. humile* mediated by “native ants” and *P. imparis*, we explicitly included these as paths in the model (Rosseel 2012).

## RESULTS

### *Changes in the distribution of L. humile and native ant species over the survey period*

The distribution of *L. humile* retracted by 30% and 27% from 1994 to 2020 in fall and spring surveys, respectively (Fig. 1;  $Z_{\text{fall}} = -4.73$ ,  $P_{\text{fall}} < 0.01$ ;  $Z_{\text{spring}} = -4.39$ ,  $P_{\text{spring}} < 0.01$ ). By contrast, the distribution of *P. imparis* in the spring expanded 70% during this time period (Fig. 1;  $Z_{\text{spring}} = 2.05$ ,  $P_{\text{spring}} = 0.04$ ). The distributions of *Camponotus* spp. in the fall, and *M. andrei* in both fall and spring surveys declined significantly (Appendix S1: Fig. S3; *Camponotus* spp.:  $Z_{\text{fall}} = -2.58$ ,  $P_{\text{fall}} = 0.01$ ; *M. andrei*:  $Z_{\text{fall}} = -2.00$ ,  $P_{\text{fall}} = 0.04$ ;  $Z_{\text{spring}} = -3.54$ ,  $P_{\text{spring}} < 0.01$ ). The distributions of *Formica* spp. and *T. sessile* did not vary systematically across the survey period in either the fall or spring surveys (Appendix S1: Fig. S3).

The distributions of *L. humile* and native ant species varied with season. The distribution of *L. humile* was

15% larger in fall than spring surveys ( $U = 503$ ,  $P < 0.001$ ; Appendix S1: Table S2; Fig. 1). The distributions of *P. imparis*, *Camponotus* spp., *Formica* spp., and *T. sessile* were 108%, 79%, 43%, and 61% larger in spring surveys than in fall surveys, respectively ( $U = 10$ , 81.5, 113.5, 136.5;  $P < 0.001$  for all) while the distribution of *M. andrei* did not differ between spring and fall ( $U = 276$ ,  $P = 0.36$ ; Appendix S1: Table S1).

Native ant species richness increased 25% and 57% over the course of the survey period for fall and spring surveys, respectively. When counts of all native species listed in Appendix S1: Table S1 were included, these trends were statistically significant only for spring surveys (Fig. 1;  $Z_{\text{fall}} = 1.75$ ,  $P_{\text{fall}} = 0.08$ ;  $Z_{\text{spring}} = 2.14$ ,  $P_{\text{spring}} = 0.03$ ). However, when rarely observed species (Appendix S1: Table S1) were excluded from the counts, richness increased significantly in both survey periods ( $Z_{\text{fall}} = 2.18$ ,  $P_{\text{fall}} = 0.03$ ;  $Z_{\text{spring}} = 2.82$ ,  $P_{\text{spring}} = 0.01$ ). Native ant community evenness (PIE) did not vary systematically in the fall or spring surveys, either when rare species were included (Fig. 1;  $Z_{\text{fall}} = 1.47$ ,  $P_{\text{fall}} = 0.14$ ;  $Z_{\text{spring}} = 0.41$ ,  $P_{\text{spring}} = 0.68$ ) or removed ( $Z_{\text{fall}} = 1.28$ ,  $P_{\text{fall}} = 0.20$ ;  $Z_{\text{spring}} = 0.36$ ,  $P_{\text{spring}} = 0.72$ ) from the analysis.

### *Effect of drought on L. humile and native ant distributions*

The distribution of *L. humile* was significantly smaller after the 2012–2015 drought than before the extended drought, with a 20% decline in distribution in fall surveys and a 28% decline in spring surveys (Appendix S1: Fig. S4;  $W_{\text{fall}} = 67$ ,  $P_{\text{fall}} = 0.01$ ;  $W_{\text{spring}} = 81$ ,  $P_{\text{spring}} = 0.01$ ). During the drought, the distribution of *L. humile* was also significantly smaller than pre-drought for spring surveys, and marginally significantly lower for fall surveys ( $W_{\text{fall}} = 58$ ,  $P_{\text{fall}} = 0.06$ ;  $W_{\text{spring}} = 56$ ,  $P_{\text{spring}} = 0.04$ ). The number of sites occupied by *P. imparis* did not vary significantly between pre-, during, and postdrought periods (Appendix S1: Fig. S4). The distribution of only one native ant species, *M. andrei*, contracted significantly after the drought, and only in spring surveys (Appendix S1: Fig. S5;  $P = 0.04$ ). Further, native ant species richness did not vary systematically in fall or spring surveys when rare species were included ( $W_{\text{fall}} = 19$ ,  $P_{\text{fall}} = 0.18$ ;  $W_{\text{spring}} = 27.5$ ,  $P_{\text{spring}} = 0.15$ ), or excluded ( $W_{\text{fall}} = 19$ ,  $P_{\text{fall}} = 0.18$ ;  $W_{\text{spring}} = 27.5$ ,  $P_{\text{spring}} = 0.015$ ). Similarly, native ant evenness did not vary systematically when rare species were included ( $W_{\text{fall}} = 23$ ,  $P_{\text{fall}} = 0.36$ ;  $W_{\text{spring}} = 40$ ,  $P_{\text{spring}} = 0.88$ ) or excluded ( $W_{\text{fall}} = 24$ ,  $P_{\text{fall}} = 0.41$ ;  $W_{\text{spring}} = 40$ ,  $P_{\text{spring}} = 0.88$ ).

### *Direct and indirect effects of climate on L. humile distribution*

The final structural equation model fit the data well ( $\chi^2 = 13.15$ ,  $df = 11$ ,  $P = 0.28$  [Grace et al. 2010]) and

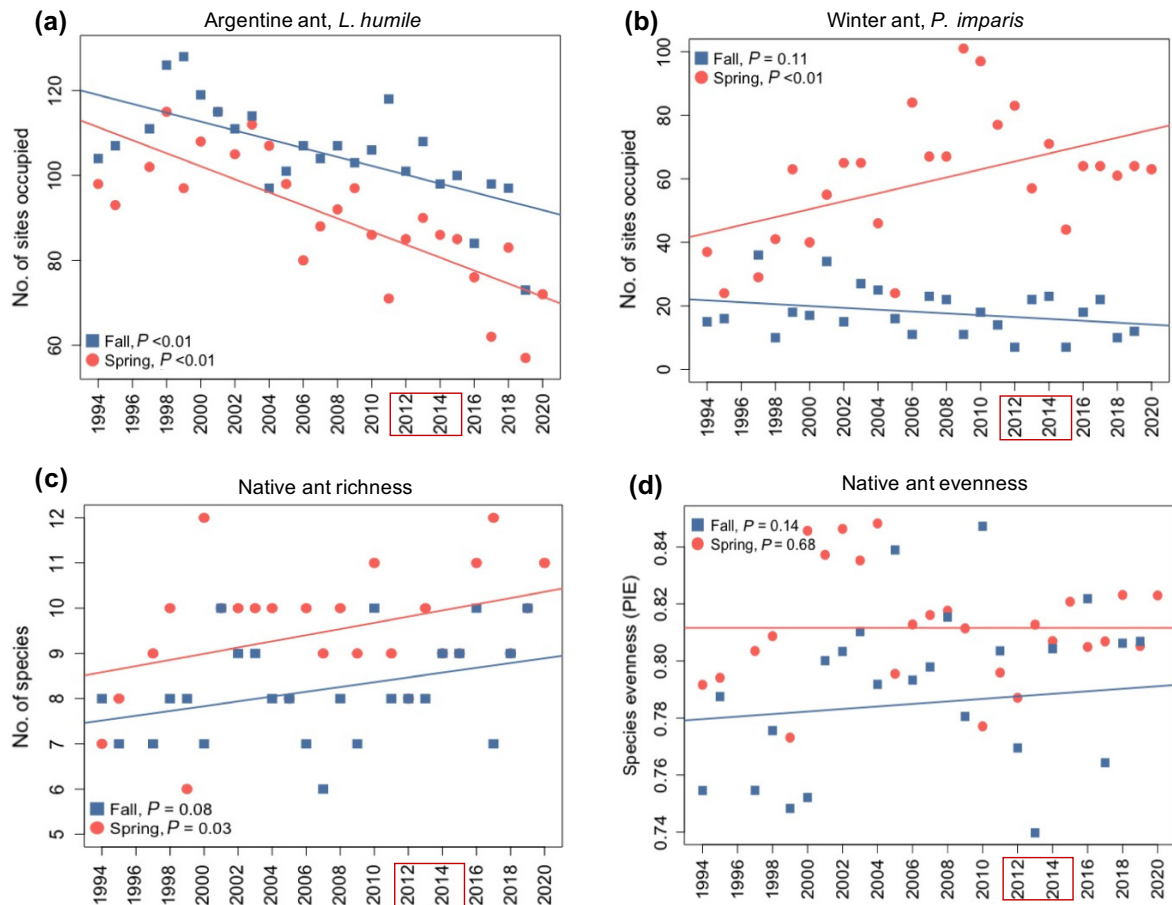


FIG. 1. Trends in (a) *Linepithema humile* and (b) *Prenolepis imparis* distributions, and (c) native ant richness and (d) evenness (Hurlbert's probability of interspecific encounter, see *Methods: Statistical Analysis*) over the survey period. The years of extreme drought (2012–2015) are shown in a red box on the x-axis. P values are obtained from modified Mann-Kendall trend tests. A line of best fit is shown on each plot.

accounted for 57% of the variation in the distribution of *L. humile* in the fall surveys (Fig. 2). The model indicated that there were direct effects of climate on fall *L. humile* distributions (Appendix S1: Table S2; Fig. 2). Four-year cumulative precipitation and maximum summer temperature had the strongest direct effect on the distribution of *L. humile*: greater cumulative precipitation and lower summer temperature extremes were associated with larger fall distributions. The relationship between the distributions of native ant species in spring and *L. humile* in the fall was positive but marginally non-significant; this effect was weaker than the effect of climate. The distribution of *P. imparis* in the spring did not significantly affect the distribution of *L. humile* in the fall, but removing this path did not improve the model ( $\chi^2 = 12.05$ ,  $df = 8$ ,  $P = 0.15$ ), and it was left in as it was biologically motivated. Indirect effects of climate on the distribution of *L. humile* mediated through the distribution of *P. imparis* and other native ant species were minimal and nonsignificant (Appendix S1: Table S2).

## DISCUSSION

Our long-term survey (1993–2020) of an ongoing biological invasion shows that the distribution of the invasive Argentine ant, *L. humile*, has retracted in response to major drought in the region. Earlier data from this survey showed that *L. humile* initially spread rapidly in the preserve, then reached a relatively stable distribution around 2001 (Ingram and Gordon 2003). Examining the entire 28 yr of the survey, including an extreme drought event (2012–2015), reveals a significant decline in *L. humile* range within the preserve associated with lower 4-yr cumulative precipitation and higher summer maximum temperature. This result is consistent with experimental and empirical evidence indicating that the activity and distribution of *L. humile* is driven by water availability (Holway 1998, Holway et al. 2002b, Menke and Holway 2006, Menke et al. 2007, Heller et al. 2008). This may be because its shallow nesting behavior renders *L. humile* particularly vulnerable to temperature extremes and desiccation (Heller and Gordon 2006).

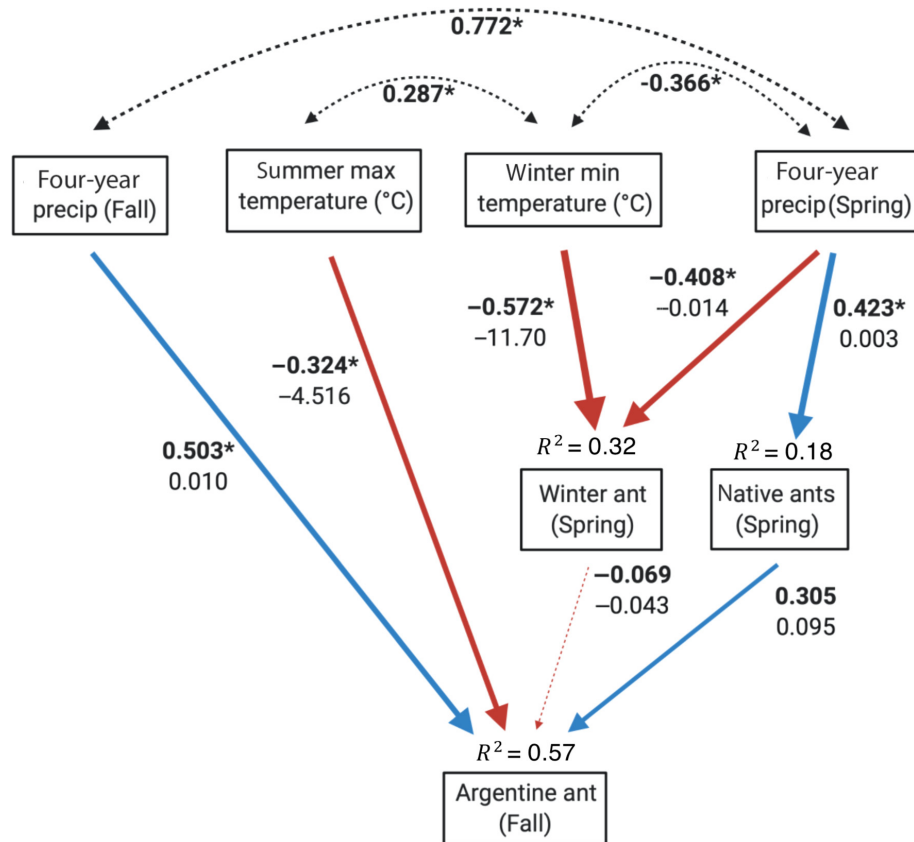


FIG. 2. Final structural equation model relating climate, spring distributions of native ants and *Prenolepis imparis*, and fall distributions of *Linepithema humile* ( $\chi^2 = 8.51$ ,  $df = 11$ ,  $P = 0.39$ ). Path coefficients are displayed next to arrows and represent the expected change in the response given a one-unit change in the predictor given the other variables. Path coefficients are either standardized by the standard deviation of the variables (bold, top), or unstandardized (bottom). Nondashed arrows and asterisks next to parameter estimates denote significant relationships ( $P < 0.05$ ). Red and blue arrows denote negative and positive relationships, respectively. Double-headed arrows represent covariances.

In contrast to *L. humile*, the distribution of the native winter ant, *P. imparis*, did not retract during or after the drought, and instead increased across the survey period, especially in the spring (Fig. 1). *Prenolepis imparis*, the winter ant, nests deep in the soil and is primarily active during the cooler and wetter winter months, making it less vulnerable than *L. humile* to drought and summer climatic extremes (Tschinkel 1987). Prior studies in the preserve have found that relative to other native ant species, *P. imparis* more frequently coexists with *L. humile*, but tends to retreat from areas with thriving *L. humile* populations (Fitzgerald et al. 2012, Fitzgerald and Gordon 2012, Gordon and Heller 2014). Relaxed competition from *L. humile*, in addition to its winter-active phenology, may have enabled the expansion of the distribution of *P. imparis* over the 28-yr survey period.

In general, other native species were also minimally impacted by the drought. Native ant richness and evenness did not vary between pre-, during, and postdrought periods, and native ant richness increased over the course of the survey period. However, one native ant species, *Messor andrei*, had a significantly smaller

distribution after the drought compared to pre-drought, and the distributions of both *M. andrei* and *Camponotus* spp. contracted over the survey period (Appendix S1: Figs. S3, S4). The decline in the distribution of *M. andrei*, the only seed-harvesting ant species commonly detected in the survey, could have been driven by reduced seed availability due to drought (Jacobsen and Pratt 2018). Greater competition with neighboring conspecific colonies due to reduced seed availability (Rissing 1988) may have restricted the foraging range of *M. andrei* colonies (Brown and Gordon 2000), so colonies were not able to obtain sufficient food. This would need to be tested by measuring seed abundance, which was not measured in this study. Prior laboratory experiments have found native ant species in the region have relatively high heat and desiccation tolerance compared to *L. humile* (Witt and Giliomee 1999, Holway et al. 2002b). Our results indicate that extreme drought conditions may be tolerable to many but not all native ant species.

Native ants did not hinder *L. humile* invasion success (Table S2, Fig. 2). Rather, we found that the distribution of *L. humile* was positively (but not significantly)

associated with those of native ants in the previous season. This is consistent with the results of previous studies in this region, showing positive or negligible associations between native ant species and *L. humile* activity, survival, or spread (Holway 1998, Holway et al. 2002b) and those of a global analysis of the factors governing *L. humile* spread, which found that native ant diversity had a weak effect on *L. humile* distributions in climatically suitable regions (Roura-Pascual et al. 2011). We found that although *P. imparis* expanded significantly during the survey period, the distribution of *P. imparis* in the spring had a negligible impact on the distribution of *L. humile* in the subsequent fall (Fig. 2), indicating that direct competition from *P. imparis* was not a strong driver of *L. humile* range contraction. *Prenolepis imparis*, which has a unique chemical defense against *L. humile*, may primarily deploy this secretion for nest protection rather than to facilitate colonization of new sites (Sorrells et al. 2011, Gordon and Heller 2014). Previous studies showed that *L. humile* was less likely to colonize sites previously occupied by *P. imparis*, especially at densely shaded sites that provide high-quality habitat for *P. imparis* where *L. humile* presence is typically low (Fitzgerald and Gordon 2012). It may be that *P. imparis* spread was not a strong driver of *L. humile* range contraction because *P. imparis* was opportunistically expanding into sites that *L. humile* vacated due to drought, rather than outcompeting *L. humile* at these sites.

Consistent with the minimal effect of native ants on the distribution of *L. humile*, we found no evidence for an indirect effect of climate mediated through changes in the distribution of the five most common native ant species (*P. imparis*, *Camponotus* spp., *Formica* spp., *M. andrei*, and *T. sessile*; Appendix S1: Table S2). Studies on other taxa have arrived at mixed conclusions on the relative strength of direct effects of climate and indirect effects through species interactions (Diamond et al. 2017). Further mechanistic studies of climate change impact involving *L. humile* are needed to clarify whether, and under what community contexts, species interactions may influence future invasion success.

Overall, our results suggest that decreasing annual precipitation and more frequent climatic extremes, as projected for this region under climate change, may restrict the local spread of *L. humile*. More generally, we demonstrate that both long-term climate trends and episodic climate extremes can alter invasion dynamics over time. Understanding the ongoing impact of climate change on the behavior and distributions of invasive species is critical for prioritizing and planning management actions aimed at preserving biodiversity and ecosystem function.

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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/ecy.3476/supinfo>

## OPEN RESEARCH

Data (Couper et al. 2021) are available through the Stanford Digital Repository (SDR) in the Stanford University Libraries. <https://purl.stanford.edu/dg373xs8682>