Biol Invasions (2025) 27:123
https://doi.org/10.1007/s10530-025-03583-8

ORIGINAL PAPER

# Historical resurveys provide support for abiotic limits to Argentine ant invasion in southern California

**Shane Hathaway · Sean B. Menke ·**
**David A. Holway**

Received: 17 December 2024 / Accepted: 26 March 2025 / Published online: 19 April 2025
© The Author(s) 2025

**Abstract** Predicting where introduced species will establish and spread remains a central goal of invasion biology. While climate data are often used to forecast potential occurrence at regional scales, environmental filtering can limit susceptibility to invasion at finer scales. Factors underlying such filtering are important to identify, especially when they influence spread into protected areas set aside for conservation. Useful information about factors limiting invasion can be obtained from historical resurveys. Between 2022 and 2024, we used pitfall traps and visual surveys to resurvey 111 sampling points in two protected areas in coastal San Diego County, California (Torrey Pines State Reserve and the Point Loma Ecological Conservation Area) that were originally surveyed for the non-native Argentine ant between 1995 and 1997. The multi-decade time span between the surveys coupled with the observed distributional limits, which have either contracted (Torrey Pines) or appear static (Point Loma), indicate that the Argentine ant has reached the limits of its ability to invade these sites. At Torrey Pines the soil types with the lowest water retention values were the least invaded in the original survey and were overrepresented among retractions observed in the resurvey. These findings are consistent with experimental work demonstrating the central role of soil moisture in limiting Argentine ant spread in seasonally dry areas. Variation in precipitation combined with changes in human water use will likely continue to influence the distribution of the Argentine ant in semiarid regions. These results generally illustrate the value of historical resurveys in clarifying limits to invasion.

**Keywords** California · Formicidae · Historical resurvey · Introduced species · Invasion · *Linepithema humile* · Soil type

## Introduction

Forecasting potential distributions for introduced species has long served the important and practical goal of clarifying where invaders are most likely to establish and spread (Peterson 2003; Thuiller et al. 2005; Jiménez-Valverde et al. 2011). Ecological niche modelling, in particular, plays an important role in risk assessments for introduced species. The usefulness of this approach critically depends on identifying the environmental factors that govern occurrence and

---

**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1007/s10530-025-03583-8.

S. Hathaway · S. B. Menke
Department of Biology, Lake Forest College, Lake Forest, IL 60045, USA

D. A. Holway (✉)
Department of Ecology, Behavior and Evolution, University of California at San Diego, La Jolla, CA 92093, USA
e-mail: dholway@ucsd.edu

understanding how the relative importance of different factors can change with the spatial grain of analysis (Menke et al. 2009; Manzoor et al. 2018).

As for invasions generally, studies on introduced ants commonly employ ecological niche models to predict regional occurrence (Morrison et al. 2004; Roura-Pascual et al. 2004; Menke et al. 2009; Bertelsmeier et al. 2013; Kumar et al. 2015; Nair et al. 2024). Such modelling efforts typically use climate data (temperature and precipitation) to forecast where ant invasions are most likely to occur and how these distributions may change under different climate change scenarios. Within regions deemed to have suitable climates to support introduced ants, environmental filtering can influence occurrence at finer spatial scales (Menke et al. 2009). The factors underlying such filtering are critical to understand because they can influence susceptibility to invasion at the ecosystem scale. Many protected areas set aside for conservation, for example, have environments suitable for introduced species yet are not currently invaded, suggesting future challenges resulting from the spread of such species (Liu et al. 2020). Experiments (Menke et al. 2007; Tschinkel and King 2017), longitudinal studies (Holway 1998; Sanders et al. 2001; Krushelnycky and Gillespie 2010; Naughton et al. 2020; Couper et al. 2021), and historical resurveys (Morrison 2002; Hoffmann and Parr 2008; Wetterer 2017; Menke et al. 2018; Probert et al. 2020) can all contribute to an understanding of susceptibility to invasion at fine spatial scales.

Here we use multi-decade, resurvey data to examine changes in Argentine ant occurrence in two protected areas in coastal southern California. Ecological niche modelling studies have identified climatic factors that shape regional scale occurrence of this invader (Roura-Pascual et al. 2004; Menke et al. 2009; Nair et al. 2024). In semiarid regions a positive association between the Argentine ant and water is also long recognized (Tremper 1976; Ward 1987) and supported by field experiments that employ irrigation to encourage spread in seasonally dry environments (Menke and Holway 2006; Menke et al. 2007). Moreover, long-term-studies in California invoke dry conditions as a key factor limiting invasion. For example, Menke et al. (2018) and Couper et al. (2021) both identified the 2012–2015 drought, which was the most severe drought experienced in California in several centuries (Belmecheri et al. 2016), as a factor impacting site-level Argentine ant persistence in natural areas. In urban areas in San Diego, Menke and Holway (2020) speculated that localized retractions of the Argentine ant could partly be the result of reductions in residential irrigation driven by increasing costs of water in this region. Given that climates within the Argentine ant's expansive introduced range vary from wet temperate climates (southern Japan, southeastern North America) to semiarid Mediterranean climates (coastal southern California), the importance of soil moisture in limiting the distribution of this species likely increases with decreasing annual precipitation, the length of the dry season, and, at finer spatial scales, heterogeneity in soil moisture resulting from how different soil types retain water.

Given variation in water retention capacities across soil types, soils should play a role in limiting Argentine ant spread in seasonally dry environments. Not surprisingly, a number of authors describe associations between Argentine ant occurrence and soil-type variation, but no published studies have established a mechanistic link between these two variables. Tremper (1976) speculated that the apparent association between alluvial soils and Argentine ant presence in northern California might be related to this soil type being easy for ants to excavate. In southern Portugal Way et al. (1997) qualitatively described both positive and negative associations between Argentine ant occurrence and different soil types but did not speculate on what might underlie these relationships. In coastal southern California, where soil moisture controls the spread of the Argentine ant (Menke and Holway 2006; Menke et al. 2007), soil-type heterogeneity seems likely to influence the local distribution of this invader and how it might change in response to drought conditions.

We resurveyed two protected areas in coastal southern California (i) to determine how the distribution of the Argentine ant has changed over a multi-decade time span, and (ii) to assess if distributional changes are associated with soil-type variation. Between 2022 and 2024, we resurveyed 111 sampling points at Torrey Pines State Reserve (King 1999) and the Point Loma Ecological Conservation Area (Suarez, A.V., *unpublished*) that were originally surveyed for the Argentine ant between 1995 and 1997. This resurvey differs from others conducted in this region (Menke and Holway 2020; Achury et al. 2021) in that the sampling was conducted at a finer spatial scale; our data thus allow for an analysis of site-level patterns of spread. The multi-decade time span separating the original surveys from the subsequent resurveys is sufficient (based on rates of Argentine ant spread by budding) to reveal limits to Argentine ant invasion (if present) and to determine if these limits reflect underlying abiotic factors (e.g., soil-type variation).

## Methods

### Study sites

The two locations resurveyed in this study both lie along the coastline of San Diego County, California. Torrey Pines State Reserve (TPSR) protects 809 ha of coastal sage scrub and chaparral and is managed by the California State Park Service. The Point Loma Ecological Conservation Area (PLECA) preserves 263 ha of coastal sage scrub habitat under the joint management of the National Park Service and the US Navy. At both locations human visitation is restricted to existing roads and trails, and perennial vegetation is almost entirely native. Away from the immediate coastline, natural vegetation at PLECA and TPSR is bordered by irrigated areas with ornamental vegetation. GPS coordinates and maps associated with the original surveys (King 1999, Suarez, A.V., *unpublished*) allowed us locate original sampling locations. GPS coordinates for all resurveyed sites are listed in Appendix 1 (TPSR) and Appendix 2 (PLECA).

### Survey/resurvey methods

Pitfall traps were used to survey ants in the original surveys and the subsequent resurveys. At TPSR pitfall traps were deployed at every sampling point ($n = 95$) on the following dates: fall 1995—summer 1997 (original survey) and July 2023 (resurvey). At PLECA pitfall traps were deployed at every sampling point ($n = 16$) on the following dates: March 1996 and July 1997 (original survey) and March and July 2022 (resurvey). In the original surveys pitfall traps consisted of 240-ml glass jars, 73 × 89 mm (Qorpak, Bridgeville, PA, USA) containing a 50:50 solution of water and (non-toxic) antifreeze. For the resurveys individual pitfall traps consisted of 50-ml, plastic centrifuge tubes filled with a solution of either unscented dish soap, salt, and water (TPSR) or water and (non-toxic) antifreeze (PLECA). At each sampling point in the original surveys and the PLECA resurvey, we used five pitfall traps in a configuration resembling the five on a die with 20 m between traps on each corner and a fifth trap in the center. These traps were left open in the field for five days. For the TPSR resurvey we used three pitfall traps at each sampling point; traps were separated by 5 m and arranged in a triangle. These traps were left open in the field for two days.

Owing to methodological differences in the pitfall trap sampling between the original surveys and our subsequent resurveys, we also conducted at least two visual searches and used baits within 10 m of sampling points where the Argentine ant was detected in pitfall trap samples in the original surveys but not in the resurveys. Documentation of apparent absences represents a general challenge in historical resurveys, and repeated, point-level sampling serves as an objective and recommended method to cope with this challenge (Tingley and Beissinger 2009). Visual searching involved visiting target sampling points at both TPSR and PLECA during the spring and summer in 2023 or 2024 under weather conditions favorable for Argentine ant foraging. We visually searched for ants by examining bare ground, vegetation, and under stones. This approach is an effective means of detection for the Argentine ant (Menke et al. 2018; Menke and Holway 2020), especially in areas with open vegetation. Visual searches lasted 60 min or until the Argentine ant was detected. If the Argentine ant was not detected within 60 min, then we used four baits each consisting of c. 5 ml of cookie crumbs (Pecan Sandies, Keebler©) placed in areas of open soil. We inspected baits after 60 min.

To obtain a broader perspective regarding the distribution of the Argentine ant at TPSR and PLECA, we also surveyed sampling points that were not part of the original surveys. Appendices 1 and 2 list GPS coordinates for these additional sampling points at TPSR ($n = 16$) and PLECA ($n = 168$). At additional sampling points, we relied on visual searches (as described in the preceding paragraph) conducted in 2023 or 2024 and under weather conditions favorable for Argentine ant foraging to determine the presence or absence of this species. Sites identified as absences were in most cases occupied by native ants sensitive to Argentine ant displacement.

### Statistical analysis

We created maps of TPSR and PLECA in ESRI Arc GIS that included the following information: Argentine ant presence or absence at all sampling points where pitfall trapping was conducted, Argentine ant presence or absence at additional sampling points (surveyed in 2023 and 2024), distance to the nearest paved road, and soil type coverage. The layers used to make these maps are accredited to the California Department of Parks and Recreation Park Routes (Recreational Routes.gdb; www.parks.ca.gov/?page_id=29682) and the Natural Resources Conservation Service (Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture; Soil Survey Geographic (SSURGO) Database for San Diego Co., CA).

The spatial heterogeneity of soil types at TPSR combined with the number of sampling points at this location made it possible to examine associations between soil type (Table 1) and Argentine ant occurrence. We used contingency table analyses to address the following questions. (i) Were sampling points with and without the Argentine ant in the original survey independently distributed with respect to soil type? (ii) Do the observed frequencies of retractions (i.e., sampling points where the Argentine ant was detected in the original survey but not in the resurvey) in the different soil types differ from the expected frequencies based on the distribution of the Argentine ant across soil types in the original survey? We used a Welch's two-sample *t*-test to determine if sampling points with and without the Argentine ant in the original survey differed with respect to distance to the nearest paved road. We used one-way ANOVAs (i) to test if sampling points where the Argentine persisted (present in both surveys), sampling points where the Argentine ant retracted, and sampling points that were never invaded differed with respect to distance to the nearest paved road in the resurvey, and (ii) to test if sampling points in the four most common soil types and occupied by the Argentine ant in the original survey differed with respect to distance to the nearest paved road. We considered 'distance to the nearest paved road' as a variable in these analyses because introduced species in general can spread along roads. At PLECA the smaller number of sampling points in the original survey precludes us from being able to perform comparable statistical analyses. We performed all statistical analyses in R (R Core Team 2021). All data used in this study are summarized in Appendix 1 and 2.

**Table 1** Physical properties of the four most common soil types at Torrey Pines State Reserve (TPSR) and the number of sampling points in each soil type. Soil types: Corralitos loamy sand (CsD), Carlsbad gravelly loamy sand (CbC), Loamy alluvial land-Huerhuero complex, (LvF3), and Terrace escarpments (TeF). Soil water retention, the ability of soil to retain water, is a function of soil particle size, soil compaction, and percent organic matter

| | CsD | CbC | LvF3 | TeF |
|---|---|---|---|---|
| Percent sand | 81.1 | 83.5 | 100 | 100 |
| Water retention | 0.08 | 0.06 | 0.00 | 0.00 |
| Sampling points in original survey | 11 | 22 | 24 | 36 |

## Results

Resurveys of TPSR and PLECA revealed expansive areas at both locations where the Argentine ant has failed to invade over a multi-decade time scale. At TPSR, in fact, the distribution of the Argentine ant has contracted (Fig. 1, Table 2). In the original TPSR survey the Argentine ant was detected at 75% (71/95) of sampling points, whereas in the resurvey this species was only found at 46% (44/95) of sampling points (Fig. 1). Sampling points with and without the Argentine ant in the original TPSR survey did not differ with respect to distance from the nearest paved road (Welch's two-sample *t*-test: $t = 1.12$, df $= 30.88$, $P = 0.27$). Likewise, in the TPSR resurvey, the three categories of sampling points (i.e., Argentine ant always present, never present, and retraction) also did not differ with respect to distance from the nearest paved road (one-way ANOVA: $F_{2,92} = 1.31$, $P = 0.28$). The resurvey at PLECA revealed a more static pattern of occurrence (Fig. 2, Table 2): the Argentine ant was detected at 25% (4/16) of sampling points in the original survey and at 31% (5/16) of points in the resurvey (Fig. 2). Visual surveys and baiting at sampling points in 2023 and 2024 revealed Argentine ant presence at three sampling points (two at TPSR, one at PLECA) where this species was absent from

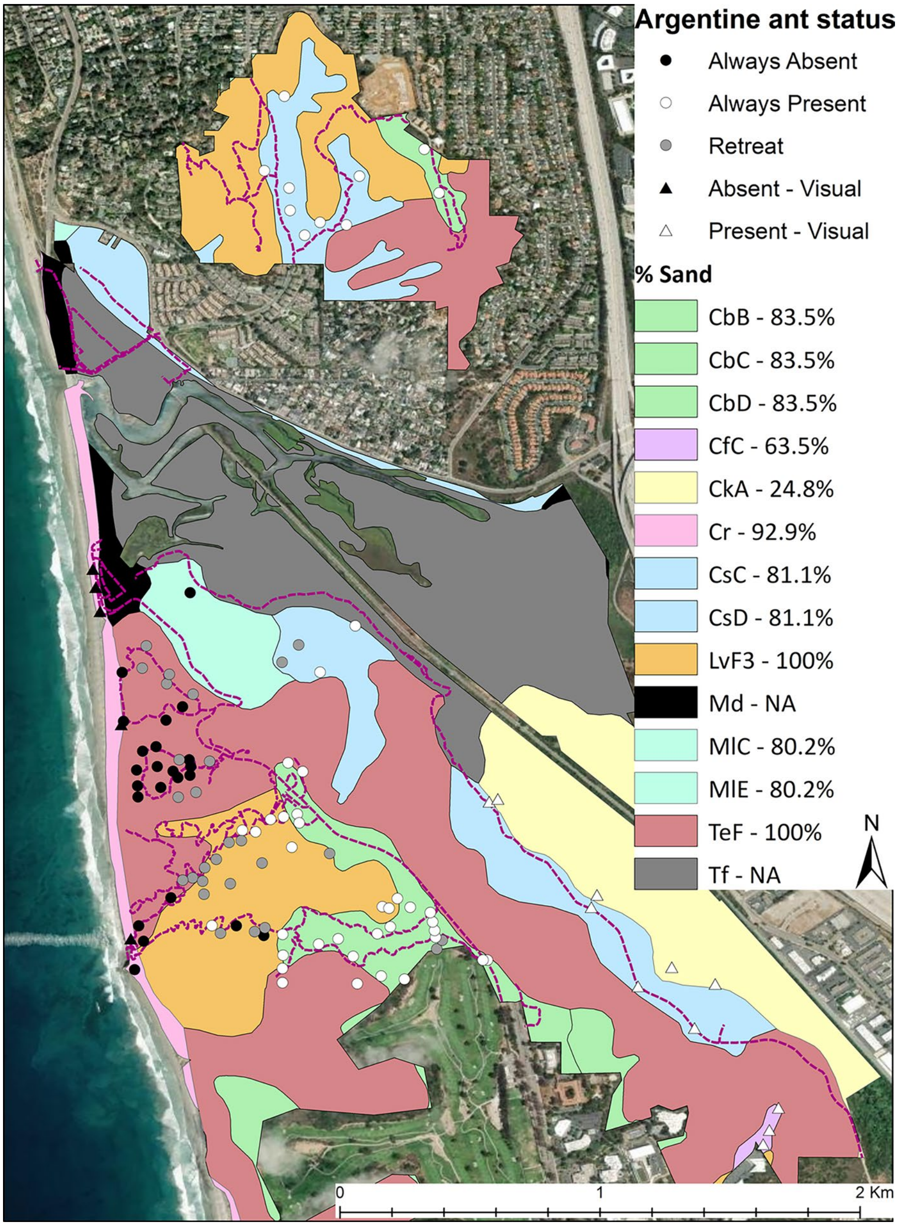


**Fig. 1** Argentine ant status at Torrey Pines State Reserve based on a historical resurvey of 95 sampling points (always present, always absent, retreat) and 16 additional sampling points surveyed between 2022 and 2024 (absent—visual, present—visual). Soil type names are as follows: Carlsbad gravelly loamy sand, 0–5% slopes (CbB), Carlsbad gravelly loamy sand, 5–9% slopes (CbC), Carlsbad gravelly loamy sand, 9–15% slopes (CbD), Chesterton fine sandy loam (CfC), Chino silt loam (CkA), Coastal beaches (Cr), Corralitos loamy sand, 5–9% slope (CsC), Corralitos loamy sand, 9–15% slopes (CsD), Loamy alluvial land-Huerhuero complex (LvF3), Marina loamy coarse sand, 2–9% slopes (MIC), Marina loamy coarse sand (MIE), and Terrace escarpments (TeF)

pitfall trap samples in the resurvey. In both resurveys, we found fewer native ant species at sampling points with the Argentine ant compared to those without the Argentine ant (Table 2).

At TPSR both the distribution of the Argentine ant and how it changed over time depended on soil type. Sites with and without the Argentine ant in the original survey were unequally distributed with respect to soil type (Fig. 3A; Fisher exact test: $P < 0.0001$). All sampling points in soil types CbC and CsD were invaded, whereas more than half of sampling points in soil type TeF were uninvaded (Fig. 3A). In the resurvey, the observed frequencies of retractions in different soil types differed from the expected frequencies based on the pattern of Argentine ant occurrence across soil types in the original survey (Fig. 3B; Chi-square test: $X^2 = 10.67$, df $= 3$, $P = 0.014$). We observed fewer retractions than expected in soil types CbC and CsD and more than expected in soil types LvF3 and TeF (Fig. 3B). Sampling points

**Table 2** (i) Argentine ant occurrence and (ii) native ant richness at Torrey Pines State Reserve (TPSR) and the Point Loma Ecological Conservation Area (PLECA). Argentine ant occurrence values are based on the original surveys and subsequent resurveys. Native ant richness values are based on subsequent resurvey data only. For each location, richness estimates with different superscripts significantly differ: TPSR (one-way ANOVA: $F_{2,92}= 26.59$, $P< 0.00001$) and PLECA (Welch's two-sample *t*-test: $t= -3.56$, df $=5.054$, $P= 0.016$)

(i) Number of sampling points occupied by the Argentine ant

| Location | Present both surveys | Absent both surveys | Expansions | Retractions |
|---|---|---|---|---|
| TPSR | 44 | 24 | 0 | 27 |
| PLECA | 4 | 11 | 1 | 0 |

(ii) Mean (± SE) number of native ant species per sampling point

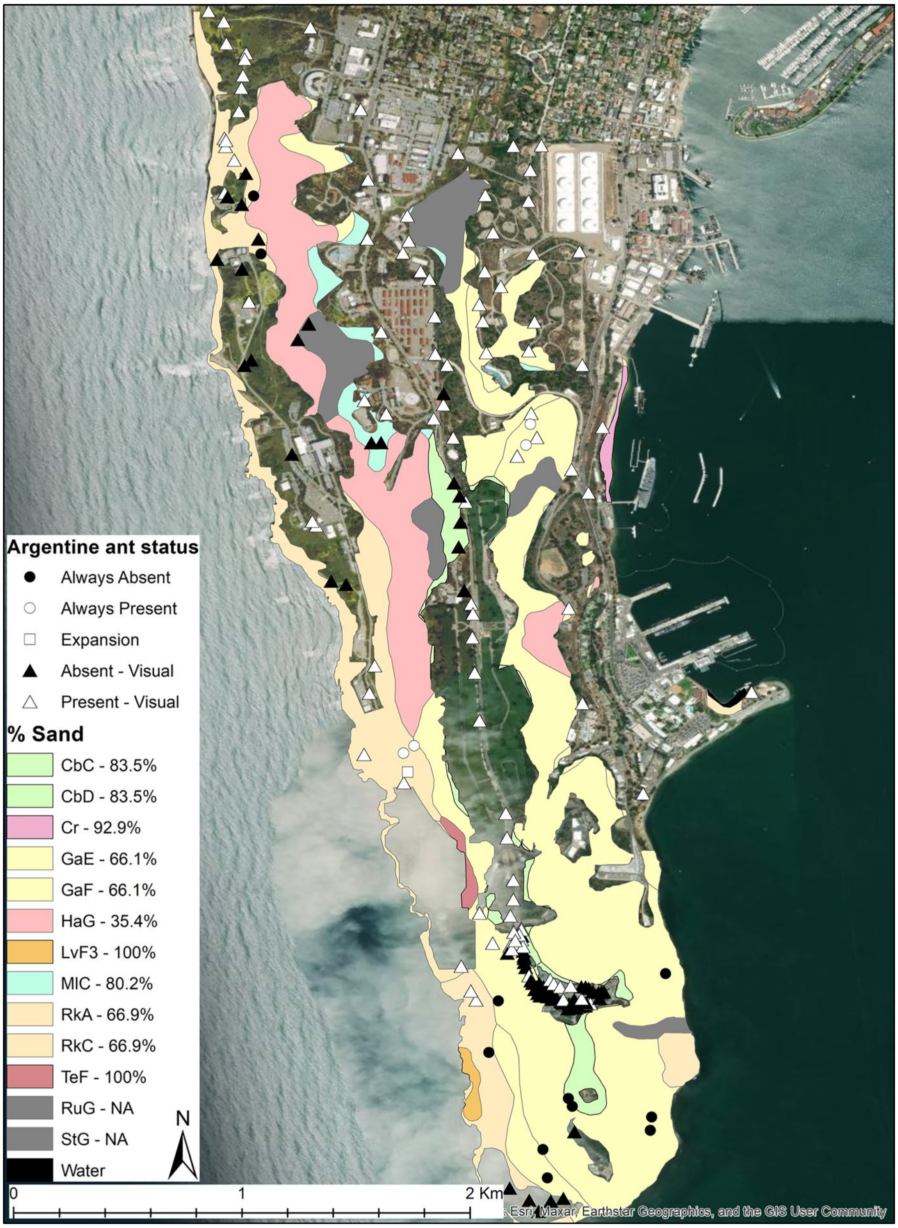
| Location | Present both surveys | Absent both surveys | Expansions | Retractions |
|---|---|---|---|---|
| TPSR | $1.34 \pm 0.24^{a}$ | $3.58 \pm 0.28^{b}$ | n/a | $3.63 \pm 0.29^{b}$ |
| PLECA | $1.50 \pm 0.50^{a}$ | $3.55 \pm 0.28^{b}$ | $0.0 \pm 0.0$ | n/a |

in the different soil types did not differ with respect to their distance to the nearest paved road (one-way ANOVA: $F_{3,88}= 2.37$, $P= 0.076$). Soil type heterogeneity is lower at PLECA compared to TPSR, but the uninvaded sampling points at the tip of the peninsula (Fig. 2) were mostly in relatively unconsolidated, sandy soil and distant from sources of irrigation (e.g., Fort Rosecrans National Cemetery). Invaded sampling points at PLECA (Fig. 2), in contrast, were all in close proximity to (or downslope from) sources of irrigation.

## Discussion

The resurveys conducted in this study revealed unambiguous limits to Argentine ant invasion. The time span separating the original surveys from the subsequent resurveys coupled with the observed distributions, which have either contracted (TPSR) or appear static (PLECA), provide compelling evidence that the Argentine ant hasn't continued to spread at these locations. This conclusion is of course predicated on the assumption that temporal patterns of Argentine ant occurrence at sampling points are representative of changes that may have occurred elsewhere at each location. That said, the interval of time between the surveys and the resurveys would have been more than sufficient for this species to spread throughout uninvaded portions of TPSR and PLECA based on published rates of spread by budding (Holway 1998). These findings are noteworthy given that the Argentine ant is widespread and abundant in coastal southern California (Suarez et al. 1998; Holway 2005; Mitrovich et al. 2010; Hanna et al. 2015; Menke and Holway 2020; Achury et al. 2021), especially along the immediate coast (Richmond et al. 2019). Our results further point to an association between soil type variation and Argentine ant invasion success.

The observational nature of this study precludes a conclusive determination of what factors act to limit Argentine ant spread. Past experimental studies, however, demonstrate that abiotic factors can play a central role (Menke and Holway 2006; Menke et al. 2007). Menke and Holway (2006), for example, used drip irrigation to elevate soil moisture levels in dry areas contiguous with sites invaded by the Argentine ant. Irrigation stimulated Argentine ant spread, and the cessation of irrigation led to a symmetrical and opposite response. The experiments described in Menke and Holway (2006) seem particularly relevant to the present study given that one replicate was in PLECA and a second was 4 km east of TPSR. Our observation that soil type influenced both susceptibility to invasion and persistence provides an additional line of evidence supporting the hypothesis that dry soils limit spread. The two soil types that were the least invaded in the original survey and also the most overrepresented in terms of the number of observed retractions (LvF3, TeF) have a lower ability to retain water (and a higher fraction of sand) compared to the other two soil types (CbC, CsD) (Table 1). Elsewhere in this region, the Argentine ant typically does not



Esri, Maxar, Earthstar Geographics, and the GIS User Community

**Fig. 2** Argentine ant status at Point Loma Ecological Conservation Area based on a historical resurvey of 16 sampling points (always present, always absent, retreat) and 80 additional sampling points surveyed between 2022 and 2024 (absent—visual, present—visual). Soil type names are as follows: Carlsbad gravelly loamy sand, 5–9% slopes (CbC), Carlsbad gravelly loamy sand, 9–15% slopes (CbD), Coastal beaches (Cr), Gaviota fine sandy loam, 9–30% slopes (GaE), Gaviota fine sandy loam, 30–50% slopes (GaF), Hambright gravelly clay loam, 30–75% slopes (HaG), Loamy alluvial land-Huerhuero complex (LvF3), Marina loamy coarse sand, 2–9% slopes (MIC), Reiff fine sandy loam, 0–2% slopes (RkA), Reiff fine sandy loam, 5–9% slopes (RkC), Rough broken land (RuG), Steep gullied land (StG), and Terrace escarpments (TeF)

occur in areas with sandy soils that are not irrigated or that lack a source of naturally occurring water.

Alternative explanations for abiotic limits to invasion cannot be ruled out given the data presented here but seem less likely. Soil moisture variation, for example, could indirectly influence the Argentine ant through its effects on plant growth (Menke and Holway 2006), which could in turn enhance habitat suitability. At both TPSR and PLECA, however, we observed no obvious qualitative association between Argentine ant persistence and plant assemblage composition. Biotic resistance in the form of interspecific competition from native ants also seems unlikely to explain the observed distributional limits. Studies throughout California report evidence for interspecific competition between native ants and the Argentine ant (Tremper 1976; Ward 1987; Human and Gordon 1996; Holway 1998, 2005; Suarez et al. 1998; Sanders et al. 2001; Mitrovich et al. 2010; Hanna et al. 2015; Naughton et al. 2020), but multi-year

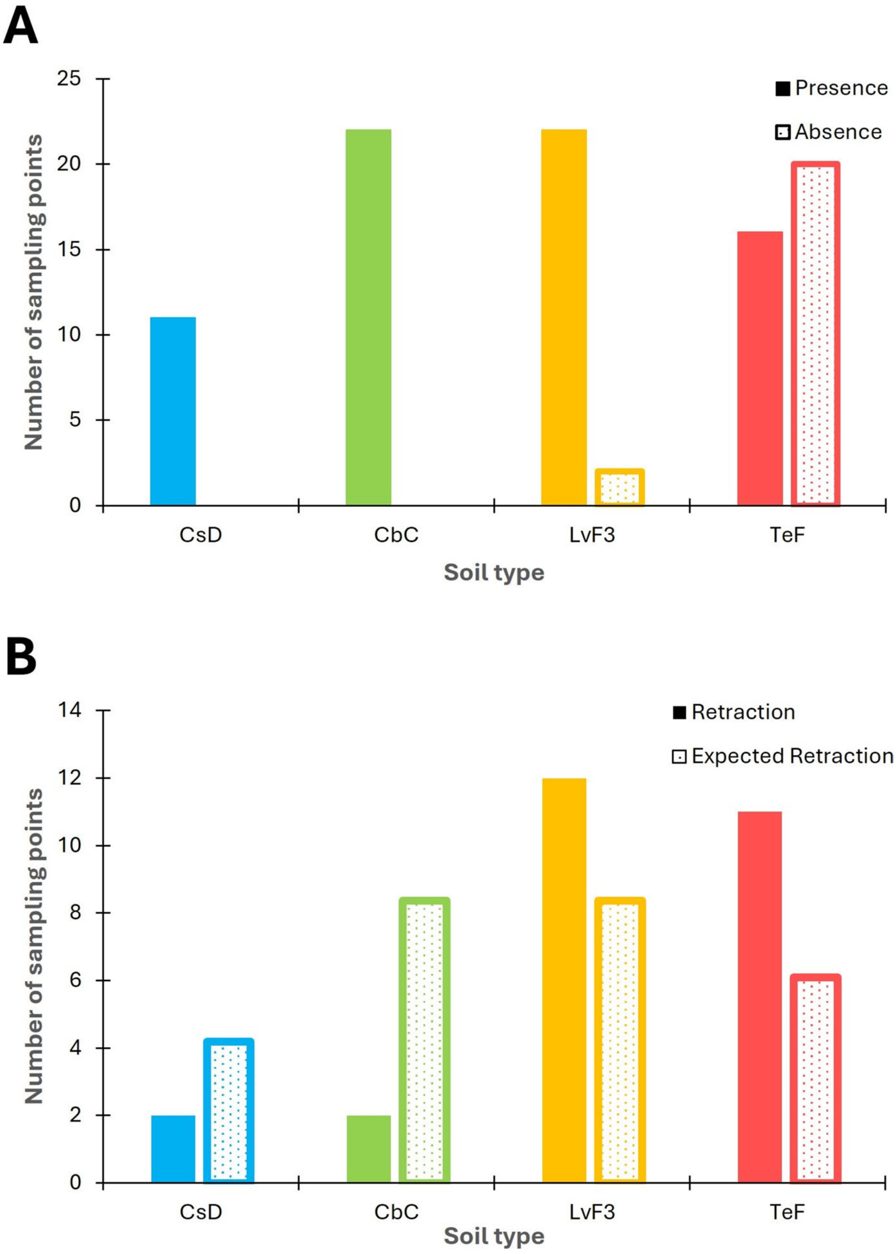


**Fig. 3** Argentine ant occurrence and soil type at Torrey Pines State Reserve (TPSR). **A** The frequency of Argentine ant presences (closed bars) and absences (stippled bars) in the original survey across four different soil types. **B** The observed frequency of retractions (closed bars) across four different soil types and the expected frequency of retractions (stippled bars) based on the distribution of the Argentine ant across soil types in the original survey

studies also document the active displacement of native ants as Argentine ant invasion fronts advance into abiotically suitable natural areas (Erickson 1971; Holway 1998; Sanders et al. 2001; Tillberg et al. 2007; Naughton et al. 2020). Moreover, experimental removal of native ants from an abiotically unsuitable areas does not result in Argentine ant expansion (Menke et al. 2007). Lastly, the native ant species most common at TPSR (King 1999) and PLECA (Suarez, A.V., *unpublished*), are primarily species, or congeners of species, that the Argentine ant displaces in other locations (Menke et al. 2018; Naughton et al. 2020).

Introduced ant populations can decline in abundance and contract in distribution over time (Cooling et al. 2011; Cooling and Hoffmann 2015; Lester and Gruber 2016; Tartally et al. 2016). While large-scale surveys are better suited to address population-level declines compared to small-scale surveys like the present one, we do not believe that the distributional limits observed in the present study represent local manifestations of large-scale declines. At TPSR, for example, where we observed retractions at more than a third of formerly occupied sampling points (Table 1), the Argentine ant remains abundant in riparian vegetation bordering Los Peñasquitos Creek in the southeastern portion of the reserve. At PLECA, additional sampling conducted in 2023 and 2024 (but not between 1995 and 1997) revealed that the Argentine ant occurs widely at this location (Fig. 2). Moreover, recently conducted resurveys conducted at broader spatial scales in this region found no evidence of regional Argentine ant decline (Achury et al. 2021; Menke and Holway 2020).

Inadequate soil moisture could hinder invasion by other invaders that cannot tolerate dry conditions. Staubus et al. (2020), for example, found that dry conditions were associated not only with decreased Argentine ant invasion but decreased invasion of other non-native arthropods as well. Restoration efforts that alter stream flow or employ irrigation should consider risks posed by invasion of non-native species that benefit from altered physical conditions. At both TPSR and PLECA, reductions in the use of irrigation (e.g., for plant restoration efforts) over the past two decades may have contributed to the patterns reported in this study. Conservation of native arthropods in semiarid regions might thus benefit from risk assessments that consider how moisture-loving introduced species may be limited by dry conditions.

**Acknowledgements** Funding for this research was provided Lake Forest College (SBM), the National Science Foundation Long-term Research in Environmental Biology 1654525 (DAH), CESU award P21 AC10870-00 from the National Park Service (DAH), and Interagency Agreement 3790 NRM12800 from the California State Parks Service (SBM & DAH). We would like to thank A. Adornato, P. Liss, K. Lombardo, L. Pandori, T. Philippi, M. Ready, C. Saban, P. Simpson, D. Smith, C. Stafford, M. Stepek, and A.V. Suarez for help with this study.

**Data availability** The datasets used in the current study are all summarized in the submitted appendices.

**Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

## References

Achury R, Holway DA, Suarez AV (2021) Pervasive and persistent effects of ant invasion and fragmentation on native ant assemblages. Ecology. https://doi.org/10.1002/ecy.3257

Belmecheri S, Babst F, Wahl ER, Stahle DW, Trouet V (2016) Multi-century evaluation of Sierra Nevada snowpack. Nat Clim Chang 6:2–3. https://doi.org/10.1038/nclimate2809

Bertelsmeier C, Luque GM, Courchamp F (2013) Global warming may freeze the invasion of big-headed ants. Biol Invasions 15:1561–1572. https://doi.org/10.1007/s10530-012-0390-y

Cooling M, Hartley S, Sim DA, Lester PJ (2011) The widespread collapse of an invasive species: argentine ants (*Linepithema humile*) in New Zealand. Biol Let 8:430–433. https://doi.org/10.1098/rsbl.2011.1014

Cooling M, Hoffmann BD (2015) Here today, gone tomorrow: declines and local extinctions of invasive ant populations in the absence of intervention. Biol Invasions 17:3351–3357. https://doi.org/10.1007/s10530-015-0963-7

Couper LI, Sanders NJ, Heller NE, Gordon DM (2021) Multiyear drought exacerbates long-term effects of climate on an invasive ant species. Ecology 102:e03476. https://doi.org/10.1002/ecy.3476

Erickson JM (1971) The displacement of native ant species by the introduced Argentine ant *Iridomyrmex humilis* Mayr. Psyche 78:257–266

Hanna C, Naughton I, Boser C, Holway DA (2015) Testing the effects of ant invasions on non-ant arthropods with high-resolution taxonomic data. Ecol Appl 25:1841–1850. https://doi.org/10.1890/14-0952.1

Hoffmann BD, Parr K (2008) An invasion revisited: the African big-headed ant (*Pheidole megacephala*) in northern Australia. Biol Invasions 10:1171–1181. https://doi.org/10.1007/s10530-007-9194-x

Holway DA (1998) Factors governing rate of invasion: a natural experiment using Argentine ants. Oecologia 115:206–212. https://doi.org/10.1007/s004420050509

Holway DA (2005) Edge effects of an invasive species across a natural ecological boundary. Biol Cons 121:561–567. https://doi.org/10.1016/j.biocon.2004.06.005

Human KG, Gordon DM (1996) Exploitation and interference competition between the invasive Argentine ant, *Linepithema humile*, and native ant species. Oecologia 105:405–412. https://doi.org/10.1007/BF00328744

Jiménez-Valverde A, Peterson AT, Soberón J, Overton JM, Aragón P, Lobo JM (2011) Use of niche models in invasive species risk assessments. Biol Invasions 13:2785–2797. https://doi.org/10.1007/s10530-011-9963-4

King JL (1999) The invasion of the Argentine ant, *Linepithema humile*, into coastal sage scrub habitat in southern

California: the ecology, limitations to invasion and impact on native ant and arthropod diversity. MS thesis, University of California, San Diego.

Krushelnycky PD, Gillespie RG (2010) Sampling across space and time to validate natural experiments: an example with ant invasions in Hawaii. Biol Invasions 12:643–655. https://doi.org/10.1007/s10530-009-9471-y

Kumar S, LeBrun EG, Stohlgren TJ, Stabach JA, McDonald DL, Oi DH, LaPolla JS (2015) Evidence of niche shift and global invasion potential of the tawny crazy ant, *Nylanderia fulva*. Ecol Evol 5:4628–4641. https://doi.org/10.1002/ece3.1737

Lester PJ, Gruber MAM (2016) Booms, busts and population collapses in invasive ants. Biol Invasions 18:3091–3101. https://doi.org/10.1007/s10530-016-1214-2

Liu X, Blackburn TM, Song T, Wang X, Huang C, Li Y (2020) Animal invaders threaten protected areas worldwide. Nat Commun 11:2892. https://doi.org/10.1038/s41467-020-16719-2

Manzoor SA, Griffiths G, Lukac M (2018) Species distribution model transferability and model grain size – finer may not always be better. Sci Rep 8:7168. https://doi.org/10.1038/s41598-018-25437-1

Menke SB, Fisher RN, Jetz W, Holway DA (2007) Biotic and abiotic controls of Argentine ant invasion success at local and landscape scales. Ecology 88:3164–3175. https://doi.org/10.1890/07-0122.1

Menke SB, Holway DA (2006) Abiotic factors control invasion by Argentine ants at the community scale. J Anim Ecol 75:368–376. https://doi.org/10.1111/j.1365-2656.2006.01056.x

Menke SB, Holway DA (2020) Historical resurvey indicates no decline in Argentine ant site occupancy in coastal southern California. Biol Invasions 22:1669–1679. https://doi.org/10.1007/s10530-020-02211-x

Menke SB, Holway DA, Fisher RN, Jetz W (2009) Characterizing and predicting species distributions across environments and scales: Argentine ant occurrences in the eye of the beholder. Glob Ecol Biogeogr 18:50–63. https://doi.org/10.1111/j.1466-8238.2008.00420.x

Menke SB, Ward PS, Holway DA (2018) Long-term record of Argentine ant invasions reveals enduring ecological impacts. Ecology 99:1194–1202. https://doi.org/10.1002/ecy.2200

Mitrovich MJ, Matsuda T, Pease KH, Fisher RN (2010) Ants as a measure of effectiveness of habitat conservation planning in Southern California. Conserv Biol 24:1239–1248. https://doi.org/10.1111/j.1523-1739.2010.01486.x

Morrison LW (2002) Long-term impacts of an arthropod-community invasion by the imported fire ant, *Solenopsis invicta*. Ecology 83:2337–2345. https://doi.org/10.2307/3072064

Morrison LW, Porter SD, Daniels E, Korzukhin MD (2004) Potential global range expansion of the invasive fire ant, *Solenopsis invicta*. Biol Invasions 6:183–191. https://doi.org/10.1023/B:BINV.0000022135.96042.90

Nair RR, Gurvich DE, Pereyra M, Srsic AN (2024) Clandestine travelers, a boon for south and a bane for north? Warming-induced shifts in global invasion potential of Argentine ants. Biol Invasions 26:3369–3392. https://doi.org/10.1007/s10530-024-03389-0

Naughton I, Boser C, Tsutsui ND, Holway DA (2020) Direct evidence of native ant displacement by the Argentine ant in island ecosystems. Biol Inv 22:681–691. https://doi.org/10.1007/s10530-019-02121-7

Peterson AT (2003) Predicting the geography of species' invasions via ecological niche modeling. Q Rev Biol 78:419–433. https://doi.org/10.1086/378926

Probert AF, Ward DF, Beggs JR, Allison-Maxwell W, Stanley MC (2020) Invasion patterns of non-native ants in natural ecosystems in warm, temperate New Zealand. N Z J Ecol 44:3400. https://doi.org/10.20417/nzjecol.44.6

R Core Team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Richmond JQ, Matsuda T, Brehme CS, Perkins EE, Fisher RN (2019) Predictability of invasive Argentine Ant distribution across Mediterranean ecoregions of southern California. Western North American Naturalist 81:243–256. https://doi.org/10.3398/064.081.0208

Roura-Pascual N, Suarez AV, Gómez C et al (2004) Geographical potential of Argentine ants (*Linepithema humile* Mayr) in the face of global climate change. Proc R Soc Lond Ser B Biol Sci 271:2527–2535. https://doi.org/10.1098/rspb.2004.2898

Sanders NJ, Barton KE, Gordon DM (2001) Long-term dynamics of the distribution of the invasive Argentine ant, *Linepithema humile*, and native ant taxa in northern California. Oecologia 127:123–130. https://doi.org/10.1007/s004420000572

Staubus WJ, Bird S, Meadors S, Meyer WM (2020) Distributions of invasive arthropods across heterogeneous urban landscapes in southern California: aridity as a key component of ecological resistance. InSects 10:29. https://doi.org/10.3390/insects10010029

Suarez AV, Bolger DT, Case TJ (1998) Effects of fragmentation and invasion on native ant communities in coastal southern California. Ecology 79:2041–2056. https://doi.org/10.1890/0012-9658(1998)079[2041:EOFAIO]2.0.CO;2

Tartally A, Antonova V, Espadaler X, Csosz S, Czechowskiet W (2016) Collapse of the invasive garden ant, *Lasius neglectus*, populations in four European countries. Biol Invasions 18:3127–3131. https://doi.org/10.1007/s10530-016-1227-x

Thuiller W, Richardson DM, Pysek P et al (2005) Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. Glob Change Biol 11:2234–2250. https://doi.org/10.1111/j.1365-2486.2005.001018.x

Tillberg CV, Holway DA, LeBrun EG, Suarez AV (2007) Trophic ecology of Argentine ants in their native and introduced ranges. Proc Natl Acad Sci 104:20856–20861. https://doi.org/10.1073/pnas.0706903105

Tingley MW, Beissinger SR (2009) Detecting range shifts from historical species occurrences: new perspectives on old data. Trends Ecol Evol 24:625–633. https://doi.org/10.1016/j.tree.2009.05.009

Tremper BS (1976) Distribution of the Argentine ant, *Iridomyrmex humilis* Mayr, in relation to certain native ants in California: ecological, physiological, and behavioral aspects. PhD Dissertation, University of California, Berkeley

Tschinkel WR, King JR (2017) Ant community and habitat limit colony establishment by the fire ant, *Solenopsis invicta*. Funct Ecol 31:955–964. https://doi.org/10.1111/1365-2435.12794

Ward PS (1987) Distribution of the introduced Argentine ant (*Iridomyrmex humilis*) in natural habitats of the lower Sacramento Valley and its effects on the indigenous ant fauna. Hilgardia 55(2):1–16. https://doi.org/10.3733/hilg.v55n02p016

Way MJ, Cammell ME, Paiva MR, Collingwood CA (1997) Distribution and dynamics of the Argentine ant (*Linepithema* (*Iridomyrmex*) *humile* (Mayr)) in relation to vegetation, soil conditions, topography, and native competitor ants in Portugal. Insectes Soc 44:415–433. https://doi.org/10.1007/s000400050062

Wetterer JK (2017) Invasive ants of Bermuda revisited. J Hymenopteran Res 54:33–41. https://doi.org/10.3897/jhr.54.11444

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.