



# Direct evidence of native ant displacement by the Argentine ant in island ecosystems

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Received: 13 April 2019 / Accepted: 1 November 2019  
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**Abstract** Ecological impacts associated with ant introductions have received considerable attention, but most studies that report on these impacts contrast species assemblages between invaded and uninvaded sites. Given the low inferential power of this type of space-for-time comparison, alternative approaches are needed to evaluate claims that ant invasions drive native species loss. Here, we use long-term data sets from two different Argentine ant eradication programs on the California Channel Islands to examine how the richness and composition of native ant assemblages change before and after invasion (but prior to the initiation of treatments). At four different sites on two different islands, pre-invasion native ant assemblages closely resembled those at uninvaded (control) sites in terms of species richness, species composition, and the presence of multiple indicator species. Invader arrival coincided with large (> 75%) and rapid (within 1 year) declines in species richness, shifts in species

composition, and the loss of indicator species. These impacts will hopefully be reversed by the recolonization of formerly invaded areas by native ant species following Argentine ant treatment, and long-term studies of native ant recovery at these sites are ongoing. Unchecked spread of the Argentine ant on other islands in this archipelago, however, poses a grave threat to native ants, which include a number of endemic taxa.

**Keywords** Displacement · Long-term data · *Linepithema humile* · Recovery · Resistance · Island

## Introduction

Are introduced species the drivers of biodiversity loss? One approach to addressing this question employs long-term data sets to examine how native species assemblages change before, during, and after an introduced species invades an ecosystem. If an assemblage lacks resistance (Knapp et al. 2001), invader arrival will coincide with the loss of native species and accompanying shifts in species composition. The generality of this type of phenomenon would be reinforced if pre-invasion assemblages resemble those from comparable sites lacking the invader. Long-term data sets that capture the establishment and spread of an invader incorporate an important element of realism lacking in many small-scale, short-term

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experiments (Knapp et al. 2001; Krushelnycky and Gillespie 2010; Kumschick et al. 2014).

Ants commonly feature in studies that quantify how ecosystems respond to (Lawton et al. 1997; Liu et al. 2016) and recover from (Majer and Nichols 1998) environmental change (Kaspari and Majer 2000; Underwood and Fisher 2006). Ecological impacts associated with ant invasions have received particular attention (Holway et al. 2002; Lach et al. 2010). Research on the Argentine ant (*Linepithema humile*), for example, made up 20% of the studies (and 30% of the data) in a recent global meta-analysis of the ecological effects of terrestrial invertebrate invasions (Cameron et al. 2016). Reductions in native ant diversity may be the most widely reported impact of Argentine ant invasions with numerous studies documenting this phenomenon primarily in California (Tremper 1976; Ward 1987; Human and Gordon 1997; Holway 1998a; Suarez et al. 1998; Holway 2005; Mitrovich et al. 2010; Hanna et al. 2015) but elsewhere as well (Lach 2007; Estany-Tigerström et al. 2010). Most of this evidence, however, consists of observational comparisons of native ant assemblages between invaded and uninvaded sites (Holway et al. 2002; Cameron et al. 2016). This type of space-for-time comparison does not by itself establish causation, does not allow for the random assignment of each replicate to different experimental groups, and implicitly assumes that sites only differ with respect to the presence or absence of the invader (Krushelnycky and Gillespie 2010; Kumschick et al. 2014). These limitations could be problematic if unmeasured environmental gradients influence the vulnerability of native ant assemblages to invasion.

Of the arsenal of experimental and observational approaches used to quantify invasion impacts (Didham et al. 2005; Kumschick et al. 2014), long-term data sets that follow invasions over time can be used to evaluate whether or not invaders cause declines in native species diversity and abundance. Although the use of long-term data sets in this context is subject to some of the same limitations inherent in observational comparisons of invaded and uninvaded sites (Kumschick et al. 2014), this approach can provide a valuable complement to observational comparisons (Krushelnycky and Gillespie 2010). The Argentine ant is well suited to this type of study given that colony reproduction occurs by budding, which makes it possible to track expanding invasion fronts as they

move into areas occupied by native ants (Erickson 1971); other introduced ants are also amenable to this approach (Porter et al. 1988; Hoffmann and Parr 2008). Studies on the Argentine ant that have followed invasion fronts over time have focused on the spatial pattern of spread (Crowell 1968; Erickson 1971), the factors controlling its rate (Holway 1998b), and how trophic position changes as a function of time since invasion (Tillberg et al. 2007). Sanders et al. (2003) used a 7-year record of Argentine ant invasion in northern California to document that pre-invasion native ant assemblages do not differ from those present at sites that lacked the Argentine ant in terms of species richness and that these assemblages changed within a year after invasion to become species poor and to exhibit co-occurrence values that are less segregated compared to pre-invasion assemblages. To date, however, no long-term study on this system has explicitly examined how the species composition of pre-invasion and post-invasion native ant assemblages compares with that of uninvaded reference sites. This data gap thus leaves open the question of whether or not sites that become invaded by the Argentine ant differ from those that are not invaded in terms of the native ant species present. Given the prominence of the Argentine ant as a widespread and abundant invader (Holway et al. 2002; Lach et al. 2010; Cameron et al. 2016), additional information concerning how native species assemblages change before and after invasion seems warranted (Krushelnycky and Gillespie 2010).

Here, we use data from two different Argentine ant eradication programs on the California Channel Islands (Boser et al. 2017; Merrill et al. 2018) to examine how native ant richness declines and how the composition of these assemblages changes before and after invasion. In anticipation of the start of these eradication programs, the authors established plots that have been annually sampled for ants in a standardized manner with the eventual goal of quantifying the reassembly of native ant communities following large-scale Argentine ant removal, and long-term studies of native ant recovery at these sites are ongoing. Here, we primarily report data from a set of plots that were invaded prior to the initiation of treatments but after long-term monitoring began. This multi-year data set provides clear evidence (1) that pre-invasion, native ant assemblages did not differ in richness or composition from those present at

uninvaded reference plots, and (2) that native ant assemblages quickly lost most of their species soon after invader arrival and from then on resembled those from plots that were invaded prior to the start of monitoring. These results corroborate differences documented between invaded and uninvaded plots in the same system (Hanna et al. 2015) and illustrate the value of using multiple approaches to document the ecological effects of invasion.

## Methods

We conducted fieldwork on three different islands on the California Channel Islands, which are an eight-island archipelago off the coast of southern California. We primarily conducted fieldwork for this study on Santa Cruz Island (Santa Barbara Co., CA) and San Clemente Island (Los Angeles Co., CA). Santa Cruz Island (249 km<sup>2</sup> and 30 km offshore) supports a fauna of 33 native ant species that in most respects resembles that of the adjacent mainland (Wetterer et al. 2000). San Clemente Island (148 km<sup>2</sup> and 79 km offshore) is relatively species poor with 14 native ant species, including at least two species that are endemic to the southern Channel Islands and Isla Guadalupe (Menke and Miller 1985). Argentine ant eradication programs were initiated in 2012 on Santa Cruz Island (Boser et al. 2017) and in 2013 on San Clemente Island (Merrill et al. 2018). Prior to the start of these eradication campaigns, approximately 2% of each island's area was invaded by the Argentine ant, which occupied multiple, spatially disjunct infestations on each island (Boser et al. 2018). Invaded areas encompassed a variety of habitats, including large expanses of native perennial vegetation (Hanna et al. 2015; Boser et al. 2018). Before eradication efforts began, multi-year delineation surveys revealed approximately radial patterns of Argentine ant expansion (as a result of colony budding) away from the edges of individual infestations on each island (Boser et al. 2018). To complement data from Santa Cruz and San Clemente Islands, we also include 1-year of survey data from San Nicolas Island (Ventura Co., CA). San Nicolas Island (59 km<sup>2</sup> and 85 km offshore) supports a fauna of five native ant species, and Argentine ant infestations now cover approximately one-fifth of this island's area (Boser et al. 2018). Two other non-native ant species are known from these islands:

*Cardiocondyla mauritanica* (present on all three islands) and *Nylanderia vividula* (present only on Santa Cruz Island). These two species are currently uncommon and locally distributed in human-modified environments. We have not detected either of these species on any of our long-term plots.

Long-term plots on all three islands are spatially interspersed inside and outside of multiple areas of Argentine ant infestation and extend over a relatively large area with the most distant plots on each island separated by > 8 km. On Santa Cruz and San Clemente Islands, plots conform to a replicated, before-after, control-impact paired series (BACIPS) design (Osenberg et al. 2006); each pair of plots includes an invaded plot and a control (uninvaded) plot. In this study, we primarily address how native ant assemblages have changed on four plots on Santa Cruz and San Clemente Islands (3 on Santa Cruz, 1 on San Clemente) that were invaded by the Argentine ant at different points since the start of sampling. For these plots we separately consider pre-invasion and post-invasion native ant assemblages, and hereafter refer to these plots as pre-invasion plots and post-invasion plots. Sample sizes and the number of years that each type of plot (i.e., control, invaded, pre-invasion, and post-invasion) was surveyed are summarized in Table 1. Plots invaded by the Argentine ant on Santa Cruz and San Clemente Islands are now all treated (Boser et al. 2017; Merrill et al. 2018) with the exception of the pre-invasion and post-invasion plot on San Clemente Island considered here. All data presented in this paper consist of pre-treatment data.

Long-term plot characteristics are as follows. Individual plots are circular with a 10-m radius (314 m<sup>2</sup>) and placed within spatially continuous stands of native perennial vegetation. Plots within each pair are matched as closely as possible with respect to the composition of perennial vegetation, extent of canopy closure, ground cover, slope, elevation and proximity. Plots within each pair are also positioned 100 m to  $\approx$  1 km from each other; individual plots are always > 250 m from plots in other pairs. Plots (n = 18) on Santa Cruz Island were established in 2010–2011 in stands of island scrub oak (*Quercus pacifica*); other native, perennial plants present include *Cercocarpus betuloides*, *Eriogonum arborescens*, *Heteromeles arbutifolia*, and *Rhus integrifolia*. Hanna et al. (2015) provides additional details regarding plot characteristics as well as a

**Table 1** Native ant species present on control (uninvaded), invaded, pre-invasion, and post-invasion plots on (a) Santa Cruz Island, (b) San Clemente Island, and (c) San Nicolas Island

(a) Santa Cruz Island	Control	Invaded	Pre-invasion	Post-invasion
Number of plots	n = 7	n = 8	n = 3	n = 3
Years sampled	5–6	3–5	1–4	1–3
Species richness	7.51 ± 0.37	2.28 ± 0.35	7.10 ± 0.49	1.56 ± 0.29
<i>Brachymyrmex depilis</i>	0.02 ± 0.02	–	–	–
<i>Camponotus hyatti</i>	0.21 ± 0.08	–	0.53 ± 0.24	–
<i>Camponotus maritimus</i>	0.78 ± 0.09	0.10 ± 0.05	0.78 ± 0.22	–
<i>Camponotus semitestaceus</i>	0.29 ± 0.14	–	0.28 ± 0.15	–
<i>Crematogaster marioni</i>	0.78 ± 0.09	0.04 ± 0.04	0.83 ± 0.17	–
<i>Dorymyrmex insanus</i>	0.08 ± 0.05	–	–	–
<i>Formica moki</i>	0.95 ± 0.03	0.11 ± 0.06	1.00 ± 0.00	0.33 ± 0.33
<i>Monomorium ergatogyna</i>	0.69 ± 0.10	0.44 ± 0.12	0.56 ± 0.29	0.17 ± 0.17
<i>Pheidole hyatti</i>	0.83 ± 0.07	0.03 ± 0.03	0.58 ± 0.30	–
<i>Polyergus vinosus</i>	0.07 ± 0.03	–	–	–
<i>Prenolepis imparis</i>	0.20 ± 0.07	0.16 ± 0.09	0.08 ± 0.08	–
<i>Solenopsis molesta</i>	0.88 ± 0.09	0.53 ± 0.12	0.67 ± 0.33	0.67 ± 0.33
<i>Stenamma diecki</i>	0.39 ± 0.10	0.13 ± 0.07	0.17 ± 0.17	0.11 ± 0.11
<i>Stenamma snellingi</i>	0.03 ± 0.03	0.09 ± 0.06	0.08 ± 0.08	–
<i>Tapinoma sessile</i>	0.18 ± 0.10	–	–	–
<i>Temnothorax andrei</i>	0.92 ± 0.05	0.77 ± 0.11	0.89 ± 0.11	0.89 ± 0.11
<i>Temnothorax nitens</i>	0.06 ± 0.06	0.03 ± 0.03	–	–
(b) San Clemente Island	Control	Invaded	Pre-invasion	Post-invasion
Number of plots	n = 6	n = 7	n = 1	n = 1
Years sampled	6	2–3	4	2
Species richness	3.46 ± 0.17	0.81 ± 0.14	4.00 ± 0.00	1.00 ± 0.00
<i>Aphaenogaster patruelis</i>	0.19 ± 0.07	–	1.00 ± 0.00	–
<i>Camponotus bakeri</i>	0.69 ± 0.15	–	1.00 ± 0.00	–
<i>Crematogaster marioni_nr</i>	0.18 ± 0.02	–	–	–
<i>Hypoponera</i> sp. CA01	0.05 ± 0.04	–	–	–
<i>Monomorium ergatogyna</i>	1.00 ± 0.00	0.90 ± 0.10	1.00 ± 0.00	1.00 ± 0.00
<i>Pheidole clementensis</i>	0.45 ± 0.09	–	0.25 ± 0.25	–
<i>Tapinoma sessile</i>	0.85 ± 0.08	–	0.75 ± 0.25	–
(c) San Nicolas Island	Control	Invaded	Pre-invasion	Post-invasion
Number of plots	n = 5	n = 5	n/a	n/a
Years sampled	1	1	n/a	n/a
Species richness	3.40 ± 0.40	0.60 ± 0.25	n/a	n/a
<i>Aphaenogaster patruelis</i>	1.00 ± 0.00	–	n/a	n/a
<i>Dorymyrmex insanus</i>	0.80 ± 0.00	–	n/a	n/a
<i>Monomorium ergatogyna</i>	0.80 ± 0.00	0.60 ± 0.00	n/a	n/a
<i>Tapinoma sessile</i>	0.80 ± 0.00	–	n/a	n/a

Species richness is reported as the mean ( $\pm$  SE) of time-averaged estimates for individual plots in each plot type category. For each species, table entries indicate the mean ( $\pm$  SE) proportion of plots at which that species was detected averaged over time for each plot type

n/a: not applicable

map of plot locations. Plots ( $n = 14$ ) on San Clemente Island were established in 2014 in stands of coast prickly-pear (*Opuntia littoralis*); other native, perennial plants present include *Bergerocactus emoryi*, *Calystegia macrostegia*, *Cylindropuntia prolifera*, and *Lycium californicum*. Plots ( $n = 10$ ) on San Nicolas Island were sampled in 2016; these plots were established in native vegetation primarily consisting of *Baccharis pilularis*, *Calystegia macrostegia*, *Isocoma menziesii*, and *Leptosyne gigantea*.

On Santa Cruz Island, standardized, annual sampling employs Winkler extractors, pitfall traps, and vegetation beating (additional details in Hanna et al. 2015) during 1 week in March (when litter ants are active) and 1 week in May–June (when above-ground foraging ants are active). These methods, used in combination, are considered sufficient to sample ant assemblages (Bestelmeyer et al. 2000) and minimally yield presence/absence data for each species on each plot. On the plots on San Clemente and San Nicolas Islands, the habitat is much more open than on Santa Cruz Island and lacks leaf litter. For these reasons, we used a combination of 45-min visual searches and cookie baits (i.e., one Pecan Sandies (Keebler®) shortbread cookie crumbled and evenly distributed among eight locations) to sample ants on each plot in each year. Sampling on San Clemente and San Nicolas Islands was conducted during annual visits during April–July by the senior author. These methods also yield presence/absence data for each species on each plot. Standardized sampling has revealed at least half of each island's native ant fauna; we have found 17 species on the plots on Santa Cruz Island (out of 33 species known from this island), seven species on the plots on San Clemente Island (out of 14 species known from this island), and four species on the plots on San Nicolas Island (out of five species known from this island). Species not yet encountered on these plots are either rare or restricted to other habitats (Wetterer et al. 2000, *pers. obs.*).

All statistical analyses in this study were performed in R (R Development Core Team 2016). Our analyses address how the richness and species composition of native ant assemblages changes before and after invasion by the Argentine ant. These analyses consider each of the four types of plots (i.e., control, invaded, pre-invasion, and post-invasion) as distinct categories. First, for the data sets from Santa Cruz and San Clemente Islands, we used one-sample *t*-tests to

compare (1) the richness of individual pre-invasion plots to the distribution of richness estimates on control plots, and (2) the richness of individual post-invasion plots to the distribution of richness estimates on invaded plots (see Sanders et al. (2003) for a similar analysis). Second, for the data from each of the three islands, we used paired *t*-tests to compare richness estimates between paired control and invaded plots (see Hanna et al. (2015) for a similar analysis). For both sets of analyses, the richness estimate for a given plot is a cumulative estimate based on the appropriate time span for that comparison. For example, if only 2 years of pre-invasion data exist for a particular pre-invasion plot, then we compared the cumulative richness estimate of this plot over the 2-year period with the cumulative richness estimates of control plots within that same time period. This approach ensures that all comparisons are based on richness estimates generated from equivalent levels of sampling.

To assess differences in species composition, we assembled community matrices based on presence/absence data for the native ant species detected on every plot (data pooled across years) and then used PERMANOVAs (each with 1000 permutations) to compare assemblages on invaded plots and control plots. The community matrix from Santa Cruz Island was amenable to an ordination (non-metric multidimensional scaling (NMDS)) that we used to trace how the composition of native ant assemblages on pre-invasion and post-invasion plots compared with those present on control and invaded plots. The PERMANOVAs and the ordination are based on Jaccard distances, which are suitable for binary (presence/absence) data (Anderson et al. 2011). In the PERMANOVAs, we used the 'strata' function in 'adonis' in the 'vegan' package in R (Oksanen et al. 2012) to take into account (i.e., by blocking) the spatial pairing of the plots on each island. Lastly, we used indicator species analysis (Dufrene and Legendre 1997) to identify native ant taxa that were either positively or negatively associated with invaded plots and then compared these taxa with those present on pre-invasion plots and post-invasion plots. The indicator species analyses are thus useful in that they identify the individual species responsible for assemblage-level differences in species composition. These analyses also provide a framework for predicting what species are most at risk if Argentine ant invasions are left to proceed unchecked. Indicator species analyses

were based on the community matrices for invaded and control plots on each of the three islands sampled, and we used the Holm correction to control for multiple comparisons. The indicator species analysis was run using the ‘*labdsv*’ package in R (Roberts 2012).

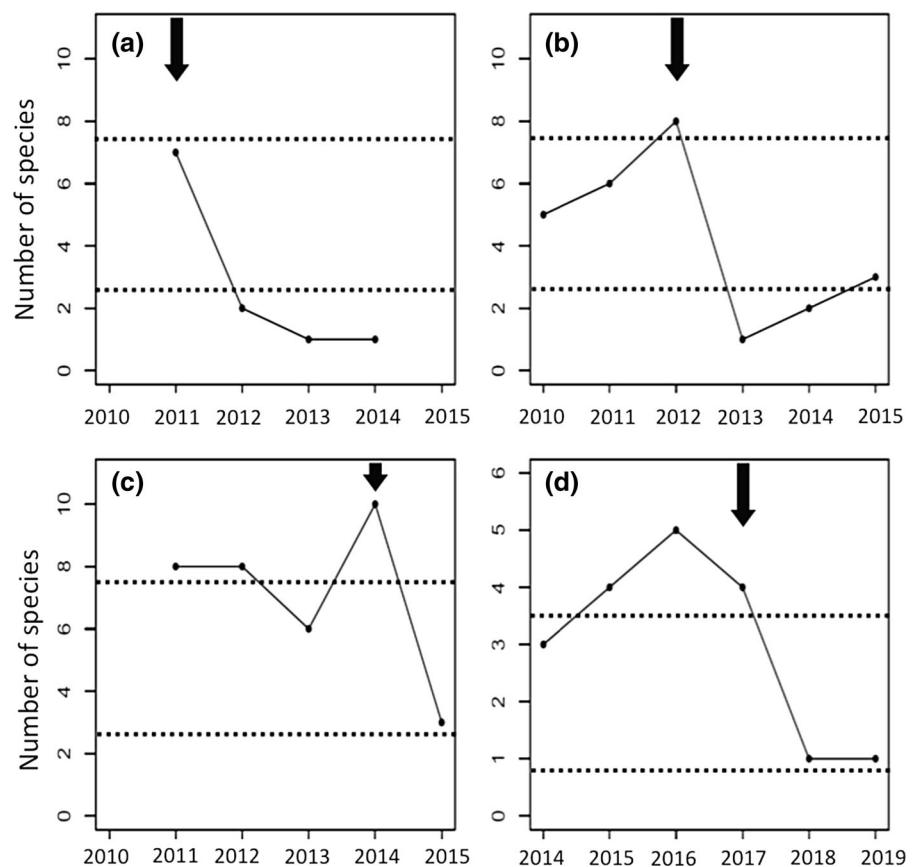
## Results

Standardized, annual sampling on long-term plots revealed how native ant species richness changed before and after invasion on Santa Cruz and San Clemente Islands (Table 1). Large (c. 75%; from  $7.10 \pm 0.49$  species to  $1.56 \pm 0.29$  on Santa Cruz Island and from  $4.00 \pm 0.00$  to  $1.00 \pm 0.00$  on San Clemente Island) and rapid (within 1 year) declines in richness coincided with the Argentine ant first appearing in each plot and were evident in four different years and on two different islands (Fig. 1). For each

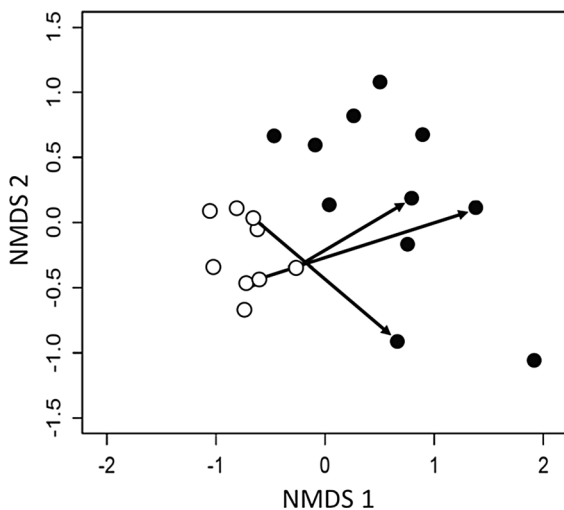
pre-invasion plot, richness estimates did not differ from those of the control plots: Santa Cruz Island (one-sample *t*-tests (for each of the three plots):  $t_7 = 0.00$ ,  $P = 1.00$ ;  $t_7 = -1.17$ ,  $P = 0.28$ ;  $t_7 = 1.00$ ,  $P = 0.35$ ) and San Clemente Island (one-sample *t* test:  $t_5 = -0.31$ ,  $P = 0.77$ ). For each post-invasion plot, richness estimates did not differ from those of invaded plots: Santa Cruz Island (one-sample *t*-tests (for each of the three plots):  $t_7 = 1.00$ ,  $P = 0.35$ ;  $t_7 = -0.42$ ,  $P = 0.68$ ;  $t_7 = 0.81$ ,  $P = 0.44$ ) and San Clemente Island (one-sample *t*-test:  $t_5 = -1.00$ ,  $P = 0.36$ ). Lastly, species richness estimates were significantly lower on invaded plots compared to those on control plots for all three islands (paired *t*-tests: Santa Cruz Island ( $t_8 = 6.70$ ,  $P < 0.001$ ), San Clemente Island ( $t_5 = 10.30$ ,  $P < 0.001$ ), and San Nicolas Island ( $t_4 = 7.48$ ,  $P < 0.002$ ).

Analyses of species composition provided additional insight into how native ant assemblages respond to Argentine ant invasion. Table 1 lists the species

**Fig. 1** Native ant richness before and after Argentine ant invasion for three plots on Santa Cruz Island (a–c) and one plot on San Clemente Island (d). Arrows indicate the year that the Argentine ant was first detected on each plot. Horizontal dashed lines indicate time-averaged mean richness on invaded (lower line) and control (upper line) plots on each island



present for each plot type. Species composition of native ant assemblages on invaded and control plots significantly differed from one another: Santa Cruz Island (PERMANOVA:  $F_{1,12} = 5.39$ ,  $P < 0.02$ ) and San Clemente Island (PERMANOVA:  $F_{1,12} = 17.58$ ,  $P < 0.02$ ). For the Santa Cruz Island data set, ordination further indicated that pre-invasion plots supported native ant assemblages similar in composition to those on control plots, whereas post-invasion plots supported native ant assemblages similar in composition to those on invaded plots (Fig. 2). Lastly, indicator species analyses identified species that were negatively associated with invaded plots (Table 2); no native ant species was positively associated with invaded plots. Indicator species consisted of above-ground foraging native ant genera (e.g., *Camponotus*, *Crematogaster*, *Pheidole*, and *Formica*) and included two species that are restricted in their distribution to the Channel Islands (Table 2). Native ant species that were negatively associated with invaded plots were mostly present in the pre-invasion fauna of plots that were later invaded, whereas these same species were mostly absent from these same plots after invasion (Table 2).



**Fig. 2** NMDS ordination (stress = 0.11) of native ant assemblages on invaded plots (filled circles) and control plots (open circles) on Santa Cruz Island. Arrows indicate shifts in species composition for three plots before (base of arrow) and after (tip of arrow) invasion by the Argentine ant (see Fig. 1). Note that one of the plots that became invaded after sampling began was invaded in the first year that this plot was sampled (2011). This plot was thereafter reclassified as an invaded plot, and we established a new control plot nearby

## Discussion

Our results demonstrate that pre-invasion native ant assemblages closely resembled assemblages on uninvaded control plots in terms of richness, composition and the presence of multiple indicator species. Invader arrival coincided with large and rapid declines in native ant species richness (Fig. 1, Table 1), shifts in species composition (Fig. 2, Table 1), and the loss of indicator species negatively associated with invaded plots (Table 2). This pattern of native ant displacement mirrors results of multi-year studies on this system conducted at sites on the California mainland (Erickson 1971; Holway 1998b; Sanders et al. 2003; Tillberg et al. 2007). As with Sanders et al. (2003), we found that pre-invasion assemblages resembled those present at plots that have not been invaded in terms of species richness; our analyses take these comparisons a step further in that we considered how the composition of pre-invasion and post-invasion assemblages changes before and after invasion. In particular, the indicator species analyses revealed close similarities in species composition between pre-invasion native ant assemblages and those at control plots and between post-invasion assemblages and those at invaded plots. Taken together, these results demonstrate that invasive ants, such as the Argentine ant, can directly displace a predictable set of native ant species as opposed merely moving into areas after native ants have disappeared for reasons unrelated to invasion.

Native ants identified as being negatively associated with the Argentine ant in this study (Table 2) exhibit overlap, at either the species or genus level, with above-ground foraging native ants that are negatively associated with the Argentine ant on the mainland (Menke et al. 2018). Most of these species are medium- to large-bodied native ant species. The displacement of such species results from the Argentine ant's competitive ability (Human and Gordon 1996; Holway 1999) and its tendency to raid native ant colonies (Zee and Holway 2006). In contrast, native ant species that persist after invasion (e.g. *Solenopsis molesta*, *Temnothorax andrei*) are primarily species with tiny workers. This size-dependent pattern of displacement is a widely noted feature of ant invasions (Ward 1987; Hoffmann et al. 1999; Tillberg et al. 2007; Le Brun et al. 2013).

The loss of native ants from our long-term study plots on Santa Cruz and San Clemente Islands will

**Table 2** Native ant species negatively associated with the Argentine ant on long-term plots on (a) Santa Cruz Island, (b) San Clemente Island, and (c) San Nicolas Island

	Indicator value	Present at ...	
		Pre-invasion plots	Post-invasion plots
(a) Santa Cruz Island			
<i>Crematogaster marioni</i>	0.89**	yes (3/3)	no (0/3)
<i>Pheidole hyatti</i>	0.89**	yes (2/3)	no (0/3)
<i>Camponotus maritimus</i>	0.73*	yes (3/3)	no (0/3)
<i>Formica moki</i>	0.73*	yes (3/3)	yes (1/3)
(b) San Clemente Island			
<i>Camponotus bakeri</i> <sup>a</sup>	1.00***	yes (1/1)	no (0/1)
<i>Tapinoma sessile</i>	1.00***	yes (1/1)	no (0/1)
<i>Pheidole clementensis</i>	0.86**	yes (1/1)	no (0/1)
(c) San Nicolas Island			
<i>Aphaenogaster patruelis</i> <sup>b</sup>	1.00**	n/a	n/a

Table entries are indicator values (and their associated level of statistical significance) from indicator species analyses. Table entries for the columns ‘present at pre-invasion plots’ and ‘present at post-invasion plots’ indicate whether or not each indicator species was present (yes or no) and also the fraction of plots at which each indicator species was present. Pre-invasion and post-invasion plots were not included in the indicator species analyses

n/a: not applicable

\*\*\*  $P < 0.001$ , \*\*  $P < 0.01$ , \* $P < 0.05$

<sup>a</sup>Endemic to San Clemente, Santa Catalina and Santa Barbara Islands

<sup>b</sup>Endemic to the southern Channel Islands and Isla Guadalupe

hopefully be reversed through island-wide removal of the Argentine ant (Boser et al. 2017; Merrill et al. 2018) and the eventual recolonization of formerly invaded areas by native ants, perhaps especially by the indicator species listed in Table 2. On San Clemente and San Nicolas Islands, indicator species negatively associated with invaded plots included species (*Camponotus bakeri*, *Aphaenogaster patruelis*) that are endemic to the southern Channel Islands (Menke and Miller 1985). These endemics seem threatened with island-level extinction on San Nicolas and Santa Catalina Islands, which support expansive Argentine ant infestations (Boser et al. 2018). The loss of native ant diversity resulting from ant invasions contributes to the broader phenomenon of introduced species driving native species loss on islands (Bellard et al. 2016).

Our results provide an example of an introduced species directly reducing native diversity, but could these findings be an artifact of particular attributes of our study sites? This possibility seems unlikely given that the pattern of Argentine ant spread on the Channel

Islands (Boser et al. 2018, this study) qualitatively and quantitatively resembles that documented on the mainland (Erickson 1971; Holway 1998b; Sanders et al. 2003; Tillberg et al. 2007). Although the Channel Islands could be less resistant to invasion compared to the mainland because they lack certain native ant species (e.g., *Liometopum occidentale*, *Solenopsis xyloni*), the Argentine ant readily displaces these species in mainland ecosystems (Ward 1987; Sanders et al. 2003; Menke et al. 2007, 2018). More generally, ant species richness does not repel the Argentine ant from invading natural areas (Holway 1998b; Sanders et al. 2003). A second possibility is that the past history of land use (e.g., introduced pigs, goats and sheep (now eradicated)) on the Channel Islands (Beltran et al. 2014; Rick et al. 2014) has somehow reduced the resistance of native ant assemblages. Densities of ant colonies, for example, might remain at depressed levels as a result of past land use. This hypothesis is hard to test directly, but ants are among the most abundant groups of arthropods on our long-term plots on Santa Cruz Island (Hanna et al. 2015), and all of our



plots are centered in large and spatially continuous expanses of native, perennial vegetation that resemble comparable habitat from well-preserved, mainland sites.

The long-term record of invasion summarized in this study validates our published comparisons of native ant assemblages from invaded and control plots on Santa Cruz Island (Hanna et al. 2015) in that differences between these two types of plot closely match the changes observed between pre-invasion plots and post-invasion plots in terms of species richness and composition. This corroboration appears further strengthened in that invaded and control plots do not differ with respect to the abundance, richness or species composition of native spiders, beetles and bark lice (Hanna et al. 2015). That is, the similarity of the non-ant arthropod assemblages present on control and invaded plots supports the assumption that invaded and control plots resembled one another except for the presence or absence of the Argentine ant. More generally, our results illustrate the value of using multiple approaches to investigate invasion impacts. Long-term data can demonstrate the causality of species displacement and coupled with observational comparisons can reveal invasion impacts that would be difficult to document using small-scale or short-term experiments (Krushelnycky and Gillespie 2010; Kumschick et al. 2014).

**Acknowledgements** Funding for this research was provided by The Nature Conservancy (DAH), US Navy (DAH), California Coastal Conservancy (DAH), National Science Foundation Long-term Research in Environmental Biology 1654525 (DAH and NDT) and US Department of Agriculture National Institute of Food and Agriculture Hatch project CA-B-INS-0087-H (NDT). We acknowledge The Nature Conservancy, Channel Islands National Park, US Navy, and University of California Natural Reserve System for granting access to field sites. The following people provided invaluable help and logistical support: M Booker, A Chisholm, D Dewey, K Faulkner, C Gagorik, C Hanna, A Hebshi, W Hoyer, L Laughrin, K Merrill, J Randall, and V Vartanian. M Booker, W Hoyer, EG Le Brun, AV Suarez, and three anonymous reviewers offered helpful comments on the manuscript.

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