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Endemism and genetic diversity of ants on the California Channel Islands: evolutionary reconstructions based on phylogenomics

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Endemism and genetic diversity of ants on the California Channel Islands: evolutionary reconstructions based on phylogenomics

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy

in

Biology

by

Ida Kristine Naughton

Committee in charge:

Professor David A. Holway, Chair
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2021

The Dissertation of Ida Naughton is approved, and it is acceptable in quality and form for publication on microfilm and electronically.

University of California San Diego

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DEDICATION

This work is dedicated to Dr. Cause Hanna in honor of his life and legacy, mentor, colleague, and friend.

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PUBLICATIONS

Naughton, I., Boser, C., Tsutsui, N. D., and Holway, D. A. 2019. Direct evidence of native ant displacement by the Argentine ant in island ecosystems. *Biological Invasions*. 1-11.

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ABSTRACT OF THE DISSERTATION

Endemism and genetic diversity of ants on the California Channel Islands: evolutionary reconstructions based on phylogenomics

by

Ida Kristine Naughton

Doctor of Philosophy in Biology

University of California San Diego, 2021

Professor David A. Holway, Chair

Islands have long been recognized for the numerous endemic species they support, and genomics tools enable rigorous tests of evolutionary processes generating endemism and diversity in island systems. Unfortunately, island diversity is subject to numerous anthropogenic threats, especially the introduction of invasive species. Here, I used data from two Argentine ant eradication programs on Santa Cruz Island and San Clemente Island, California, to examine how Argentine ant introduction affects native ant richness and shifts the composition of native ant assemblages. I found that the arrival of the Argentine ant in previously uninvaded plots coincided with large and rapid declines in ant species richness, and shifts in species composition. I also used genomics data generated through high-throughput sequencing of ultraconserved elements to (i) examine the evolutionary processes that result in endemism within four insular endemic ant taxa on the southern California Channel Islands and (ii) to conduct a multi-species comparison of genetic diversity and population genetic structure between island (Santa Cruz Island) and mainland (Lompoc Valley, California) populations of nine ant species to test for reduced levels of diversity and capacity for dispersal in insular ant populations. I found that endemism within ants on the southern Channel Islands results from both allochthonous and autochthonous evolutionary processes on multiple islands and within a single island. I also found that island populations do not differ significantly from mainland populations with respect to estimates of genetic diversity, and that mainland populations exhibit higher levels of population genetic structure consistent with lower capacities for dispersal within mainland populations. Together these studies illustrate the negative impacts of Argentine ant introductions on these unique insular assemblages, and provide novel insights into the evolutionary processes that generate endemism and genetic diversity within the ant fauna of the California Channel Islands.

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ORIGINAL PAPER

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

Ida Naughton · Christina Boser · Neil D. Tsutsui · David A. Holway

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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^2 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^2 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 Guadaupe (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^2 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^2) 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
Brachymyrmex depilis	0.02 ± 0.02	–	–	–
Camponotus hyatti	0.21 ± 0.08	–	0.53 ± 0.24	–
Camponotus maritimus	0.78 ± 0.09	0.10 ± 0.05	0.78 ± 0.22	–
Camponotus semitestaceus	0.29 ± 0.14	–	0.28 ± 0.15	–
Crematogaster marioni	0.78 ± 0.09	0.04 ± 0.04	0.83 ± 0.17	–
Dorymyrmex insanus	0.08 ± 0.05	–	–	–
Formica moki	0.95 ± 0.03	0.11 ± 0.06	1.00 ± 0.00	0.33 ± 0.33
Monomorium ergatogyna	0.69 ± 0.10	0.44 ± 0.12	0.56 ± 0.29	0.17 ± 0.17
Pheidole hyatti	0.83 ± 0.07	0.03 ± 0.03	0.58 ± 0.30	–
Polyergus vinosus	0.07 ± 0.03	–	–	–
Prenolepis imparis	0.20 ± 0.07	0.16 ± 0.09	0.08 ± 0.08	–
Solenopsis molesta	0.88 ± 0.09	0.53 ± 0.12	0.67 ± 0.33	0.67 ± 0.33
Stenamma diecki	0.39 ± 0.10	0.13 ± 0.07	0.17 ± 0.17	0.11 ± 0.11
Stenamma snellingi	0.03 ± 0.03	0.09 ± 0.06	0.08 ± 0.08	–
Tapinoma sessile	0.18 ± 0.10	–	–	–
Temnothorax andrei	0.92 ± 0.05	0.77 ± 0.11	0.89 ± 0.11	0.89 ± 0.11
Temnothorax nitens	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
Aphaenogaster patruelis	0.19 ± 0.07	–	1.00 ± 0.00	–
Camponotus bakeri	0.69 ± 0.15	–	1.00 ± 0.00	–
*Crematogaster marioni*_nr	0.18 ± 0.02	–	–	–
Hypoponera sp. CA01	0.05 ± 0.04	–	–	–
Monomorium ergatogyna	1.00 ± 0.00	0.90 ± 0.10	1.00 ± 0.00	1.00 ± 0.00
Pheidole clementensis	0.45 ± 0.09	–	0.25 ± 0.25	–
Tapinoma sessile	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
Aphaenogaster patruelis	1.00 ± 0.00	–	n/a	n/a
Dorymyrmex insanus	0.80 ± 0.00	–	n/a	n/a
Monomorium ergatogyna	0.80 ± 0.00	0.60 ± 0.00	n/a	n/a
Tapinoma sessile	0.80 ± 0.00	–	n/a	n/a

Species richness is reported as the mean (± SE) of time-averaged estimates for individual plots in each plot type category. For each species, table entries indicate the mean (± 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 (Dufrêne 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 ± 0.49 species to 1.56 ± 0.29 on Santa Cruz Island and from 4.00 ± 0.00 to 1.00 ± 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

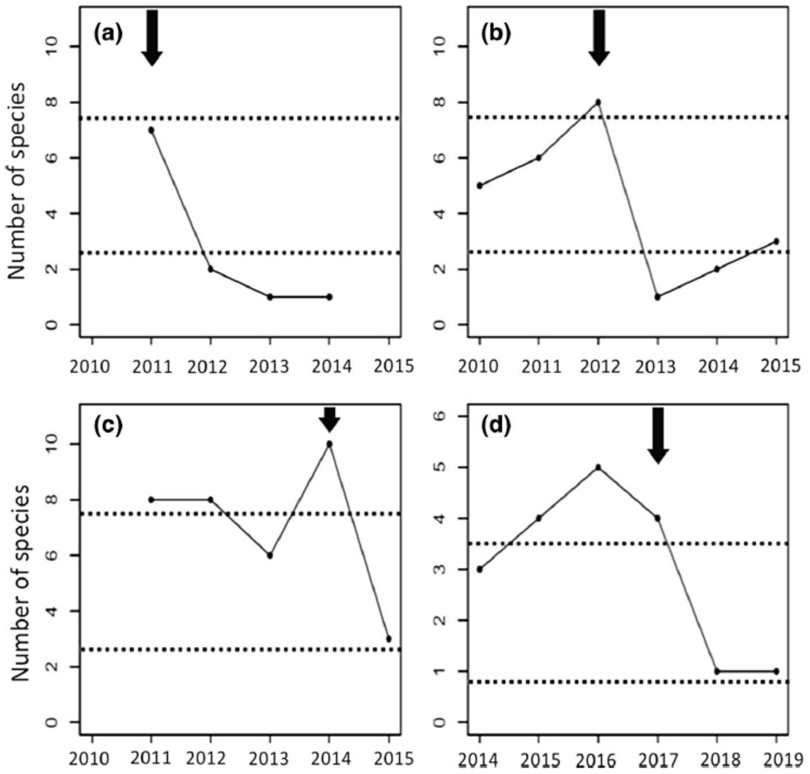

Fig. 1 Native ant richness before and after Argentine ant invasion for three plots on Santa Cruz Island (**a–c**) and one plot on San Clemente Island (**d**). Arrows indicate the year that the Argentine ant was first detected on each plot. Horizontal dashed lines indicate time-averaged mean richness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

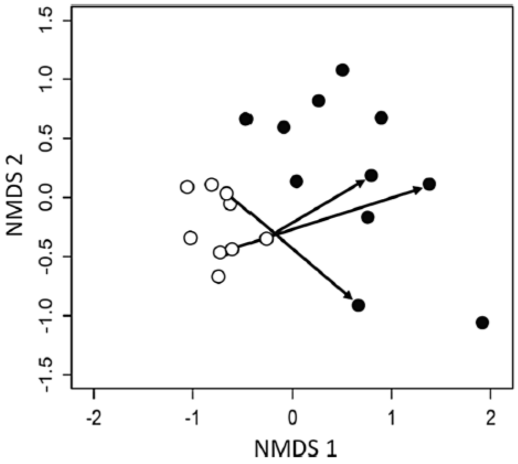

Fig. 2 NMDS ordination (stress = 0.11) of native ant assemblages on invaded plots (filled circles) and control plots (open circles) on Santa Cruz Island. Arrows indicate shifts in species composition for three plots before (base of arrow) and after (tip of arrow) invasion by the Argentine ant (see Fig. 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			
Crematogaster marioni	0.89**	yes (3/3)	no (0/3)
Pheidole hyatti	0.89**	yes (2/3)	no (0/3)
Camponotus maritimus	0.73*	yes (3/3)	no (0/3)
Formica moki	0.73*	yes (3/3)	yes (1/3)
(b) San Clemente Island			
Camponotus bakeri[a]	1.00***	yes (1/1)	no (0/1)
Tapinoma sessile	1.00***	yes (1/1)	no (0/1)
Pheidole clementensis	0.86**	yes (1/1)	no (0/1)
(c) San Nicolas Island			
Aphaenogaster patruelis[b]	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

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

[a] Endemic to San Clemente, Santa Catalina and Santa Barbara Islands

[b] 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).

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CHAPTER 2: Endemic ants from the California Channel Islands result from divergent evolutionary processes

ABSTRACT

Insular endemism can result from a variety of processes. Island endemics can be the products of post-colonization, *in situ* differentiation driven by founder effects, genetic drift, and novel selection pressures (autochthonous endemism), or they can evolve elsewhere but become restricted to islands through processes such as relictualization (allochthonous endemism). Molecular tools enable rigorous analyses of the evolutionary origins of insular endemics and can be used to distinguish between these two alternative scenarios. Here we use data obtained from high-throughput sequencing of ultraconserved elements (UCEs) to conduct phylogenomic and phylogeographic analyses of the evolutionary origins of four ant taxa endemic to the California Channel Islands: *Camponotus bakeri*, *C. yogi* nr., *C. vicinus* nr., and *Aphaenogaster patruelis*. These taxa represent multi-island (*C. bakeri*, *A. patruelis*) and single-island (*C. vicinus* nr., *C. yogi* nr.) endemics. All four of these species occur on San Clemente Island, which is isolated at the southern end of the archipelago. RAxML and SNAPP phylogenetic trees provide evidence for three different routes to endemism: *in situ* differentiation on the Channel Islands and subsequent interisland dispersal (*C. bakeri*), relictualization following the presumed extinction of an ancestral mainland population (*A. patruelis*), and *in situ* differentiation on a single island (*C. vicinus* nr., *C. yogi* nr.). Population genetic analyses and STRUCTURE plots further show that gene flow among island populations and between island and mainland populations occurs infrequently. These findings illustrate how endemic taxa from the same region can be the product of divergent

evolutionary processes. Through the use of genomics tools, our study provides new insights into the evolutionary processes that can lead to endemism in insular systems.

INTRODUCTION

Island systems are famous for supporting endemic species, especially in situations where the degree of isolation of an island system lies at the outer limits of the dispersal capacities of a particular type of organism (Lomolino et al. 2010). Insular endemics can result from a variety of processes. Colonists of remote islands, for example, can undergo *in situ* differentiation as a result of founder effects, genetic drift, and selection, and may eventually undergo speciation given a lack of gene flow from other populations (Raven et al. 1992, Jackman et al. 1999, Rees et al. 2001, Gillespie and Roderick 2002, Simon et al. 2018). Such insular endemics can represent the endpoint of taxon cycles (Wilson 1961), in which widespread ecological generalists that colonize islands subsequently undergo genetic differentiation, ecological specialization, and range contraction (Wilson 1961, Ricklefs et al. 1972, Economo and Sarnat 2012, Matos-Maravi 2018). Island endemics can also be the product of relictualization (Gillespie and Roderick 2002, Wilting et al. 2012, Kallimanis et al. 2011, Bushakra et al. 1999). Formerly widespread species distributed across mainland and near-shore island ecosystems, for example, can become isolated on islands as mainland populations suffer extinction. Such allochthonous endemics continue evolving on islands, but these taxa originated elsewhere, unlike autochthonous endemics, which are the product of post-colonization differentiation. A better understanding of endemism hinges on quantifying the relative importance of these alternative mechanisms.

Molecular tools have increasingly enabled rigorous analyses of the evolutionary origins of insular endemics (Emerson 2002, Bell et al. 2015, Claridge et al. 2017).

Phylogeographical studies that examine the evolutionary origins of insular endemics are often based on one or a few genetic loci, and commonly rely solely on mitochondrial DNA (mtDNA) genes (Rees et al. 2001, Chatzimanolis et al. 2010, Aleixandre et al. 2012). Using a small number of loci to infer the phylogeography of a lineage may be misleading, as gene trees may differ from an organismal phylogeny due to incomplete lineage sorting (Pamilo et al. 1998). In contrast, the application of multi-locus datasets acquired through next-generation sequencing can account for variation in patterns of gene inheritance in phylogeographical studies (McCormack et al. 2013). Targeted enrichment of ultraconserved elements (UCEs), for example, represents a powerful but underutilized method of acquiring sequence data of thousands of orthologous nuclear loci. This approach thus can be used to evaluate phylogeographic predictions with unprecedented amounts of genetic data (Bryson et al. 2016, Branstetter et al. 2019, Stiller et al. 2020). Phylogenomic approaches can provide unexpected insights into the evolutionary origins of insular endemics (Bell et al. 2015).

Numerically dominant in most terrestrial ecosystems worldwide, ants are a diverse group of social insects (Ward 2006) that exhibit striking variation in colony life-history strategies, morphology, and ecological roles (Hölldobler and Wilson 1990). The tendency for isolated archipelagos (e.g. Hawaii, eastern Polynesia) to lack native ant faunas (Wilson and Taylor 1967) suggests that ants exhibit only moderate capacities for overwater dispersal. Levels of endemism in ants vary across island systems worldwide (Morrison 2016), from zero endemics (Jaffe and Lattke 1994) to around ~70% of the ant fauna on Fiji representing endemics (Sarnat and Economo 2012), although some island systems remain poorly sampled (Wilson 1961, Wilson 1988, Wetterer et al. 2007). Ants helped to inspire important theories in biogeography (MacArthur and Wilson 1967, Vepsäläinen and Pisarski, 1982 Cole 1983). The taxon cycle (Wilson 1961), for example, proposes a sequence of ecological and evolutionary events that ultimately yield insular endemism (Economo and Sarnat 2012, Clouse et al. 2015, Matos-Maraví et al. 2018). In Fiji, ant lineages shift towards high-elevation (forested) habitats, ecological specialization, and rarity over time, resulting in an endemic fauna associated with primary forest habitats and narrow distributions relative to native and exotic species; these patterns are consistent with taxon cycle predictions (Economo and Sarnat 2012). Apart from examples of taxon cycle dynamics, and radiations resulting from ecological release (Sarnat and Moreau 2011), rigorous studies of the origins of insular endemics are lacking. The development of a targeted bait set of ultraconserved elements (UCEs) for ants (Branstetter et al. 2017) has enabled robust study of the phylogenetic relationships across the ant tree of life (Blaimer et al. 2018, Branstetter et al. 2019, Williams et al. 2020), but these tools are currently under-utilized in phylogeographical studies in insular systems.

The California Channel Islands (hereafter Channel Islands) are a biologically rich archipelago that consists of eight oceanic islands off of the coast of southern California (Fig.1, Table 1). The islands support numerous endemic species, and although endemic plant and vertebrate taxa are relatively well characterized (Schoenherr 2003), knowledge of the endemic insect fauna from these islands remains fragmentary (Menke and Miller 1994). Of the 52 known ant species on this archipelago, six taxa (11% of the total) appear to be species-level endemics (Ward et al., *in preparation*) and include four single-island endemics and two multi-island endemics (Fig.1). Endemics are best represented among the southern Channel Islands (Fig.1), which are far enough apart from each other and from the mainland

(Table 1) to prevent frequent colonization from other populations. Here, we focus on the phylogeography of four of these endemic taxa: *Camponotus bakeri*, *C. vicinus* nr., *C. yogi* nr., and *Aphaenogaster patruelis*. *Aphaenogaster patruelis* and *C. bakeri* are currently described species (Forel 1886, Wheeler 1904), while *C. vicinus* nr. and *C. yogi* nr. are currently undescribed. This set of species includes both multi-island endemics (*C. bakeri, A. patruelis*), and single island endemics (*C. vicinus* nr., *C yogi* nr.) on the southern Channel Islands (Fig. 1). Notably, all four species occur on San Clemente Island, which is isolated at the southern end of the archipelago.

In this study, we use phylogeographic analyses based on phylogenomic data to examine the evolutionary origins of four insular endemic ant taxa from the Channel Islands. Our core objective of this study is to determine the relative roles of autochthonous and allochthonous endemism in the formation of endemic ants from the Channel Islands. To evaluate this objective and to assess the genetic structure of these populations, we used data generated from high-throughput sequencing of ultraconserved elements (UCEs) to perform population genetic and phylogenomic analyses on the evolutionary origins of these insular endemics. Our study contributes to the growing number of studies that apply genomic datasets to investigate the evolutionary processes that can result in endemism within islands systems (Bell et al. 2015).

METHODS

Study area and sampling

Island area, interisland distances, and distances from the mainland for all eight Channel Islands and Guadalupe Island are listed in Table 1. Although none of these islands were ever connected to the mainland, the four northern Channel Islands were connected to one another as recently as the last glacial maximum. Guadalupe Island is usually not considered part of the Channel Islands given its separation from the other islands, but it shares biological affinities with the Channel Islands. We collected samples for each taxon from each island within its extant range, and at multiple locales throughout the mainland range within California (for those taxa that occur on the mainland). Sampling locations and collection dates are listed in Table S1. Collections from each sampling location consisted of workers from one colony. Samples of *Aphaenogaster patruelis* from Guadalupe Island are the lone exception; workers from several different colonies from the same general location on this island were mixed together. All specimens were placed in 95% EtOH immediately after collection.

UCE library prep and bioinformatics

To generate genetic data for this study, we conducted high throughput sequencing of UCEs. We used Qiagen DNeasy Blood & Tissue kits (Valencia, CA.) to extract total genomic DNA from one worker for each collection event listed in Table S1 (after removing gasters from samples to be sequenced). We made the following modifications to the kit protocol to optimize for RNase and small amounts of tissue: samples were first ground on a bead mill for 1 min at 3200 rpm, then 50µg RNase A and 10µL DTT were added to the lysis step. Samples were eluted in 300µL RNase/DNase free water, then concentrated to 100µL. Following extraction, samples were quantified using an Invitrogen™ Qubit™ 1X dsDNA HS, then sheared using a Bioruptor sonicator (Diagenode) for 1 min total shearing time (15 sec shearing time, 90 sec rest for four repetitions). We used Sera-Mag™ Magnetic SpeedBeads in PEG mixture to clean sheared DNA samples to retrieve desired fragment sizes (400 – 1000 bp in length). We used KAPA DNA Hyperprep kits to conduct end repair and A-tailing on each sample, then amplified each sample with unique i5 and i7 indexing primers (Illumina Tru-Seq adapters) for 12 cycles using KAPA HiFi Hotstart Ready Mix. Following index PCR, we quantified libraries and visualized each library on a gel (1.5% Agarose, 80 V for 60 min) to ensure target fragment sizes had been acquired.

To perform targeted enrichment on pooled libraries, we used a UCE bait set of custom-designed probes targeting 2,590 UCE loci in ants (Branstetter 2017). We followed library enrichment procedures for Arbor Biosciences MyBaits kit (Arbor Biosciences, Inc) to set up bait hybridization, and then hybridized RNA baits to libraries at 65C for 24 h. We amplified enriched libraries using universal Illumina primers and 18 PCR cycles, and purified PCR product using a 1.2X SPRI bead clean. To verify enrichment of our libraries, we conducted a qPCR assay (Faircloth et al. 2013a) on five pairs per each lane of sequencing of unenriched and post-enriched libraries using DyNAmo™ Flash SYBR®Green qPCR kit (Thermo Fisher Scientific) to amplify three UCEs in each library (UCE82, UCE591, UCE1481). Following qPCR verification, we sent enriched samples to the Vincent J. Coates Genomic Sequencing lab at UC Berkeley, where peak fragment size of each pool was checked on a Bioanalyzer prior to pooling at equimolar concentrations into a single lane and sequenced on an Illumina HiSeq 4000.

After sequence data were demultiplexed and converted to FASTQ format by the Vincent J. Coates Genomics Sequencing laboratory, we cleaned, assembled, and aligned sequence data using the PHYLUCE package v1.5 (Faircloth 2016). We used ILLUMIPROCESSOR (Faircloth 2013b) to clean and trim raw FASTQ reads and remove low quality reads. The read count and length measurements of trimmed reads for each sample are listed in Table S2. We used ABySS 1.5.2 (Simpson et al., 2009) with a kmer setting of 60 to assemble reads de novo. Following assembly, we used a PHYLUCE script to match assembled contigs to UCE loci, and aligned all loci in a wrapper script (phyluce_align_seqcap_align) around MAFFT v.7.130b (Katoh et al. 2002). We retained loci that contained within 75% or more of our samples and concatenated the resulting loci into a .phylip file for RAxML.

In addition to tree-based approaches, we used single nucleotide polymorphism (SNP) data to examine introgression and genetic structuring among island and mainland populations as follows. We first employed allele phasing of UCE reads, which effectively identifies variable positions within a target locus of an individual. These positions are typically lost during contig assembly, as most assembly algorithms produce only the more numerous variant while discarding alternative variants (Andermann 2019). For each sample, we mapped raw fastq reads against reference contigs and marked read duplicates with SAMtools (Li et al. 2011), added read groups with Picard (http://broadinstitute.github.io/picard/) and constructed a BAM file using bwa-mem (Li et al. 2009). We used the Phyluce script phyluce_snp_phase_uces to analyze and sort reads within the BAM file for each sample into reads for each allele. To call and extract SNPs we first aligned phased reads in Phyluce, and then used the Phyluce script phyluce_snp_screen_phased_alignments to call and extract SNPs from phased alignments. We used a custom python script (https://github.com/dportik) to extract one SNP per locus at random and concatenate SNPs into a data matrix.

Phylogenetic analyses

We constructed maximum likelihood phylogenetic trees with our concatenated UCE alignments. We used jmodeltest2 (Darriba 2012; Guindon 2003) to select the highest scoring substitution model based on the Akaike information criterion for each of our UCE alignments. We conducted a maximum likelihood analysis on the CIPRES Science Gateway (Miller et al. 2010), using the RAxML-HPC v.8 tool. We specified 1000 rapid bootstrap replicates and reconciled the best ML tree with the bootstrap replicates. We used the print branch lengths option (-k) to optimize model parameters and estimate branch lengths for bootstrapped trees.

We conducted SNP and AFLP Package for Phylogenetic (SNAPP) species tree analyses (Bryant et al. 2012) using unlinked SNP data from a subset of samples for each taxon that included two to three samples per island population. Samples used within each SNAPP tree are indicated in Table S1. We used PGDSpider v. 2.1.1.5 (Lischer and Excoffier 2012) to convert our concatenated SNP matrix into a nexus format, and then imported the aligned SNPs into BEAUTi (Bouckaert et al. 2019) to set up .xml files for the SNAPP option in BEAST 2.5 (Bouckaert et al. 2019). We used a uniform rateprior distribution for each SNAPP run, fixed the two substitution rates (“u” and “v”) at 1.0, and set the initial coalescent rate parameter to 1.0. We set the MCMC chain length to 1,000,000, and examined trace files for each run in the program Tracer 1.7.1 (Rambaut et al. 2018). For the *A. patruelis* and *C. bakeri* data sets, the effective sample size (ESS) values for each statistic exceeded 200 after our initial run with an MCMC chain length of 1,000,000. For the *C. vicinus* and *C. yogi* datasets, we re-ran the analyses until we obtained ESS values above 200 for each statistic; final MCMC chain lengths were 3,000,000 (for *C. vicinus*), and 10,000,000 for (*C. yogi*). We visually analyzed SNAPP trees in DensiTree 2.2.7 (Bouckaert 2010) and summarized maximum clade credibility trees for SNAPP tree sets of each taxon using TreeAnnotator (Drummond and Rambaut 2007).

Population admixture

We used STRUCTURE 2.3.4 (Pritchard et al. 2000) to analyze SNP data under the admixture model and to examine the degree of gene flow among lineages. We assumed different numbers of genetic demes from K = 2 to K = 6 for 100,000 generations with a burn in of 50,000 and three replicates at each value of K. We used STRUCTURE-Harvester (Earl 2012) to determine the most likely number of genetic demes based on the Evanno method (Evanno 2005). Lastly, we used Arlequin 3.5.2.2 (Excoffier et al. 2010) to determine pairwise Fst and to compute a hierarchical AMOVA for each population.

RESULTS

Phylogenetic analyses illustrate that island samples of each endemic taxon form well-supported, monophyletic clades, but these trees also suggest divergent routes to endemism (Fig. 2). The tree for *Aphaenogaster patruelis*, which lacks an extant mainland population, comprises four, well-supported monophyletic clades (Fig. 2A). These clades correspond to individual islands, except for samples from San Nicolas and Santa Barbara Island (for which the clade made up of samples from the former island is nested in within that from the latter island). As with *A. patruelis*, *C. bakeri* and island populations of *C. hyatti* form a well-supported monophyletic group made up of clades that represent individual islands (or groups of islands in the case of *C. hyatti* from the formerly inter-connected northern Channel Islands). Notably, the *C. bakeri* clade is sister to a clade comprised of all *C. hyatti* samples from the northern Channel Islands (Fig. 2B). Lastly, *C. vicinus* nr. and *C. yogi* nr. form well-supported clades that represent the single islands from which these species are known, but these taxa are distinct and distant from samples of *C. vicinus* or *C. yogi* from the northern Channel Islands (Fig. 2C-D).

SNAPP analyses based on SNP data largely corroborate the RAxML analyses by elucidating similar phylogeographic patterns between island and mainland populations (Fig. 3). For *A. patruelis,* the SNAPP tree reveals discordance at the node between San Clemente and Guadalupe Islands and also indicates some level of genetic relatedness between San Clemente and Santa Catalina Islands (Fig. 3A). The SNAPP analysis of *C. hyatti* / *C. bakeri* shows high support for a monophyletic clade representing island samples of *C. hyatti* and *C. bakeri*, but the results of this analysis are inconsistent with the RAxML analysis with respect to the placement of the *C. hyatti* population from Baja California Sur. This latter branch is sister to all mainland and island samples in the SNAPP analysis (Fig. 3B), whereas this population is sister to *C. hyatti* from southern California in the RAxML analysis (Fig. 3B). Both *C. vicinus* nr. and *C. yogi* nr. are sister to clades that include mainland and northern Channel Island *C. vicinus* and *C. yogi*; these placements are both supported by high posterior probability values (Fig. 3C-D).

STRUCTURE plots further corroborate phylogenetic analyses with respect to patterns of genetic differentiation among islands and (in the case of *Camponotus*) between island and mainland populations (Fig 4). For A. *patruelis*, STRUCTURE plots cluster together populations from Santa Barbara Island and San Nicolas Island, but also populations from San Clemente Island and Guadalupe Island (Fig. 4A). Endemic *Camponotus* also form distinctive genetic demes within the STRUCTURE analyses (Fig. 4B-D). Interestingly, samples from the *C. bakeri* population from Santa Catalina Island exhibit genetic similarity with *C. hyatti* from the mainland within the STRUCTURE plots, unlike the other two island populations of *C. bakeri*. Samples of *C. vicinus* from the northern Channel Islands are contained within the genetic deme that includes samples from the central coast of mainland

California, but samples of *C. yogi* from the northern Channel Islands appear more distinct and form a genetic deme that is distinct from mainland *C. yogi* and *C. yogi* nr. Within the samples of *C. yogi* / *C. yogi* nr., there is some evidence of gene flow between *C. yogi* nr. and *C. yogi* from the mainland.

Population genetic analyses provide additional insights into the evolutionary inter-relationships of endemic ant species (Tables 2-3). For *A. patruelis*, pairwise Fst values are lowest for island populations belonging to the same genetic demes (based on STRUCTURE) and highest between populations from Santa Catalina Island and all other islands (Table 2A). For *C. bakeri* and *C. hyatti*, pairwise Fst values were highest for comparisons involving *C. bakeri* and *C. hyatti* from the northern Channel Islands; *C. bakeri* from Santa Catalina Island exhibited the lowest pairwise Fst value with mainland *C. hyatti* (Table 2B). Pairwise Fst values between northern Channel Island populations of *C. hyatti* were the lowest inter-island comparisons (-0.045 - 0.099), revealing little genetic differentiation of these populations. For *C. vicinus* nr., Fst values were higher between this taxon and *C. vicinus* from the northern Channel Islands than between *C. vicinus* nr. and the mainland (Table 2C-D). In contrast, pairwise Fst values were lower between *C. yogi* nr. and *C. yogi* from the northern Channel Islands than between *C. yogi* nr. and mainland *C. yogi*. In the hierarchical AMOVAs for *A. patruelis*, *C. hyatti* / *C. bakeri*, and *C. yogi* nr. the largest percentage of genetic variance was found to be partitioned within populations (Table 3). In contrast, the largest percentage of genetic variance was partitioned among groups for *C. vicinus* nr., although a large percentage of variance was partitioned within populations (39.91%).

DISCUSSION

Through the use of phylogenomic data and robust mainland sampling of sister taxa, our study provides novel insights into the origins of insular endemics and illustrates that endemic taxa from the same region can result from divergent evolutionary processes. Our analyses support the notion that endemic *Camponotus* on the Channel Islands originated as endemics on the islands themselves. In contrast, our results point to an allochthonous origin for *A. patruelis,* which seems most likely to have originated from a mainland population that went extinct subsequent to colonizing Guadalupe Island and the southern Channel Islands. Population genetic analyses based on SNP data show that inter-island gene flow is infrequent, although historical patterns of inter-island dispersal differ from taxon to taxon. Inter-island dispersal subsequent to speciation appears to have contributed to the current distribution of *C. bakeri,* as evidenced by the monophyletic grouping of *C. bakeri* and all island samples of *C. hyatti*. The nested structure of the portion of the *A. patruelis* phylogeny that represents populations from Santa Barbara and San Nicolas Islands also provides evidence of inter-island dispersal, but we can't determine the origin of other island populations without samples from an extant mainland population. In contrast to inter-island dispersal or multiple island colonization events on the archipelago from the mainland, *C. vicinus* nr. and *C. yogi* nr. appear to be the products of single colonization events to San Clemente Island from the mainland. Interestingly, San Clemente Island supports all four endemic taxa in the study. Given its isolated and southerly position, San Clemente Island may represent a "dead end" to inter-island dispersal within the archipelago. Single-island endemicity on San Clemente Island is documented for other taxa other than ants as well (Dodd and Helenurm 2002, Eggert et al. 2004, Wallace et al. 2017).

Although both *C. bakeri* and *A. patruelis* both represent multi-island endemics, the routes to endemism appear divergent. The monophyletic grouping of *C. bakeri* and northern Channel Island *C. hyatti* samples in the RAxML tree and SNAPP analysis is consistent with a phylogenetic pattern resulting from a single colonization to the archipelago with subsequent dispersal between islands (Emerson et al. 2002). Given the recent proximity of the northern Channel Islands to the mainland during the last glacial maximum (Schoenherr 2003), and the relatively low Fst values between Santa Rosa and Santa Cruz Islands and the mainland, a reasonable scenario is that *C. bakeri* originated from a peripatric speciation event from northern Channel Islands *C. hyatti*. The STRUCTURE analysis for *C. bakeri* indicates gene flow from mainland *C. hyatti* to Santa Catalina Island. Gene flow from the mainland to Santa Catalina Island may account for the reciprocally monophyletic grouping of *C. bakeri* and northern Channel Islands *C. hyatti*, instead of *C. bakeri* being nested within the northern Channel Islands clade, which would be expected if *C. bakeri* originated from a peripatric speciation event from northern Channel Islands *C. hyatti* (Emerson et al. 2002).

In contrast to *C. bakeri*, our analyses provide multiple sources of evidence for an allochthonous origin of *A. patruelis* on the mainland with subsequent relictualization on the islands. We can rule out a hypothesis in which *A. patruelis* originated from a peripatric speciation event involving colonists from the northern Channel Islands, because the only congener of *A. patruelis* that occurs on the northern Channel Islands (*A. occidentalis*) is not the sister taxon to *A. patruelis* (Fig. 2A). The putative sister taxon to *A. patruelis*, *A. carbonaria*, is restricted to the cape region of Baja California Sur, and disjunct species distributions on the Baja California peninsula are observed in numerous other taxa and likely resulted from range contraction, fragmentation, and relictualization of populations along different parts of the peninsula (Johnson et al. 2002, Riddle et al. 2000). A reasonable scenario might include the most recent common ancestor of *A. patruelis* and *A. carbonaria* occurring throughout the Baja California peninsula, southern California, and southern Channel Islands and Guadalupe Island, and subsequent range contraction of the ancestral taxon resulting in the paleo-endemic formation of *A. patruelis* and *A. cabonaria*. Given that Guadalupe Island is much closer to the Baja California peninsula than the southern California Channel Islands (Table 1), it seems most likely that this ancestor also colonized Guadalupe Island directly from the Baja California mainland.

Our results provide evidence that the single-island endemics, *C. vicinus* nr. and *C. yogi* nr. originated from a direct dispersal event and subsequent *in situ* diversification on San Clemente Island. Both the RAxML and SNAPP analyses place samples of *C. vicinus* nr. and *C. yogi* nr. as sister taxa to respective monophyletic groups that include mainland and northern Channel Island *C. vicinus* and *C. yogi*; this pattern indicates that *C. yogi* and *C. vicinus* colonized the northern Channel Islands and San Clemente Island independently. Furthermore, samples of *C. vicinus* nr. and *C. yogi* nr. form distinctive genetic demes in the STRUCTURE plots, suggesting that these taxa lack ongoing gene flow from populations of *C. vicinus* and *C. yogi*. Although we cannot rule out the possibility that *C. vicinus* nr. and *C. yogi* nr. are themselves the end point of a relictualization process, our data do not support this scenario. First, given the presence of closely related congeners on the adjacent mainland and northern Channel Islands, a scenario in which these endemics differentiated from *C. vicinus* and *C. yogi* is plausible (in contrast to the geographic distribution of *A. patruelis* and sister taxa, *A. carbonaria*, for example). Furthermore, the presence of single-island endemics is not unsurprising given the biogeography of ants in the region, in which nearly one third of the ant species that occur on the archipelago are restricted to a single island (Ward et al., *in preparation*).

This study represents the first examination of the phylogeography of these unique insular endemics, and we show that island populations for all taxa are distinctive and that inter-island gene flow, and gene flow between the mainland and islands is infrequent. Although the focal islands in this study are either protected or not subject to threat of development, the endemic ants discussed in this study are also sensitive to displacement by the Argentine ant (Naughton et al. 2020), and three of the southern Channel Islands (Santa Catalina, San Nicolas, San Clemente) currently support this aggressive invader. The remaining two islands in this region that support a subset of Channel Island endemic ants are either small (Santa Barbara Island) or extremely isolated (Guadalupe Island). By revealing the genetic distinctiveness of each island population, our study provides compelling justification for the ongoing conservation projects on the southern California Channel Islands, such as the San Clemente Island Argentine ant eradication program (Merrill et al. 2019). Given the fragmentary understanding of endemism within insects on the Channel Islands, our study also highlights the importance of further studies on endemic insects of this region.

Islands have long been recognized for the numerous endemic taxa they support (Johnson et al. 1973, Whittaker and Fernández-Palacios 2007), and their evolutionary origins are increasingly clarified through the use of molecular tools and advances in phylogenetic reconstruction (Emerson et al. 2002, Emerson et al. 2005). Prominent among the theories developed to explain the origins of insular endemics is the taxon cycle (Wilson 1961, Economo and Sarnat 2012, Matos-Maravi 2018). Although our study's focus on the evolutionary relationships of endemic taxa does not allow us to address the early stages of the taxon cycle, our results are not entirely consistent with the notion of endemic taxa being ecologically specialized, rare, and products of a single insular environment given that the four taxa examined appear to result from both allochthonous and autochthonous endemism. Endemics resulting from taxon cycles tend to be restricted to high-elevation, primary habitat on large islands within an archipelago (Jønsson et al. 2014). *Camponotus bakeri* and *A. patruelis,* in contrast, occur on multiple Channel Islands in multiple habitats and tend to be common (Naughton et al. 2020). Moreover, *C. vicinus* nr. occurs at all elevations on San Clemente Island. The fourth endemic, *C. yogi* nr. does appear rare, but its sister species (*C. yogi*) is also somewhat enigmatic and infrequently collected (Creighton 1966). Our results suggest the potential importance of multiple evolutionary processes that can be revealed by further investigation into the origins of insular endemics using genomics tools.

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Chapter 2, in part, is currently being prepared for submission for publication of the material. Naughton, I., Tonione, M., Chiang, B.H., Tsutsui, N.D., Ward, P.S., Holway, D.A. The dissertation author was the primary investigator and author of this paper.

Table 2-1. Geographic characteristics of the California Channel Islands and Guadalupe Island. Blue = northern Channel Islands; orange = southern Channel Islands and Guadalupe; green = Guadalupe Island. Island ages based on estimates from Muhs et al. 2009, Muhs et al. 2014, Batiza 1977.

Island	**Area (km^2)**	**Distance (km) - Mainland**	**Distance (km) - nearest island**	**Approximate Age (my)**
San Miguel	37	42	6	1.5
Santa Rosa	217	44	6	3
Santa Cruz	249	30	8	7.5
Anacapa	2.9	20	8	6.5
San Nicolas	58	98	45	1
Santa Barbara	2.6	61	39	5
Santa Catalina	194	32	34	unknown
San Clemente	145	79	34	3
Guadalupe	98.2	241	428	7

Table 2-2. Pairwise geographical distances between islands (km) (above diagonal) and pairwise Fst values between island populations (below diagonal). **(2A)** *Aphaenogaster patruelis*, **(2B)** *C. bakeri* / *C. hyatti* **(2C)** *C. vicinus* nr. / *C. vicinus* **(2D)** *C. yogi* nr. / *C. yogi*.

2A	San Clemente	San Nicolas	Santa Barbara	Guadalupe	Santa Catalina
San Clemente		101	81	428	54
San Nicolas	0.444		50	480	102
Santa Barbara	0.395	0.124		497	58
Guadalupe	0.333	0.382	0.311		482
Santa Catalina	0.565	0.645	0.583	0.485	

2B	Santa Catalina	Santa Barbara	San Clemente	Mainland	Anacapa	Santa Rosa	Santa Cruz
Santa Catalina		58	54	33	114	167	143
Santa Barbara	0.375		81	61	68	113	91
San Clemente	0.308	0.248		83	148	190	171
Mainland	0.364	0.494	0.439		18	42	33
Anacapa	0.432	0.568	0.550	0.499			8
Santa Rosa	0.355	0.563	0.489	0.391	0.099		9
Santa Cruz	0.405	0.525	0.459	0.433	0.094	-0.045	

2C	*C. vicinus* nr. San Clemente Island	*C. vicinus* Coastal CA	*C. vicinus* Santa Cruz Island	*C. vicinus* Eastern CA
C. vicinus nr. San Clemente Island		83	171	N/A
C. vicinus Coastal CA	0.686		33	N/A
C. vicinus Santa Cruz Island	0.795	0.231		N/A
C. vicinus Eastern CA	0.623	0.378	0.471	

2D	*C. yogi* nr. San Clemente Island	*C. yogi* mainland	*C. yogi* northern Channel Islands
C. yogi nr. San Clemente Island		83	171
C. yogi mainland	0.732		33
C. yogi northern Channel Islands	0.617	0.337	

Table 2-3. Hierarchical Analysis of Molecular Variance (AMOVA) for ant species endemic to the California Channel Islands. Population number and group composition as follows: for *Aphaenogaster patruelis* populations (from five islands) in three groups (based on STRUCTURE analysis; see Fig. 3). See methods for details of the analysis. *C. bakeri* / *C. hyatti* for 7 populations and 3 groups (southern Channel Islands *C. bakeri*, Northern Channel Islands *C. hyatti*, mainland *C. hyatti*. *C. vicinus* / *C. vicinus* nr. for 4 populations (*C. vicinus* nr., Santa Cruz Island *C. vicinus*, Coastal CA *C. vicinus*, Eastern CA *C. vicinus*. and three groups (based on 3 distinct genetic demes present in the STRUCTURE analysis). *C. yogi* / *C. yogi* nr. for 3 populations (*C. yogi* nr., Northern Channel Island *C. yogi*, mainland *C. yogi*, and two groups (*C. yogi* nr., mainland and northern Channel Island *C. yogi*). df = degrees of freedom, Fst = variation distributed in subpopulations in relation to total variation observed, Fsc = variation distributed in subpopulations in relation to group variation, Fct = variation distributed in groups in relation to total variation observed. *$P < 0.05$.

	A. patruelis		***C. hyatti / C. bakeri***		***C. vicinus* nr./ *C. vicinus***		***C. yogi* nr. / *C. yogi***	
Source of variation	**df**	**Percent variation**	**df**	**Percent variation**	**df**	**Percent variation**	**df**	**Percent variation**
Among Groups	2	35.78	2	33.91	2	49.68	1	29.64
Among populations within Groups	2	15.07	4	11.63	1	10.40	3	33.81
Within Populations	61	49.13	109	54.46	26	39.91	13	36.56
Fixation Indices	Fst = 0.50851*, Fsc = .23466*, Fct = .35781		Fst = 0.45539*, Fsc = 0.17599*, Fct = 0.33907*		Fst = 0.60087* , Fsc = 0.20677*, Fct = 0.49683		Fst = 0.63443, Fsc = 0.48047*, Fct = 0.29636*	

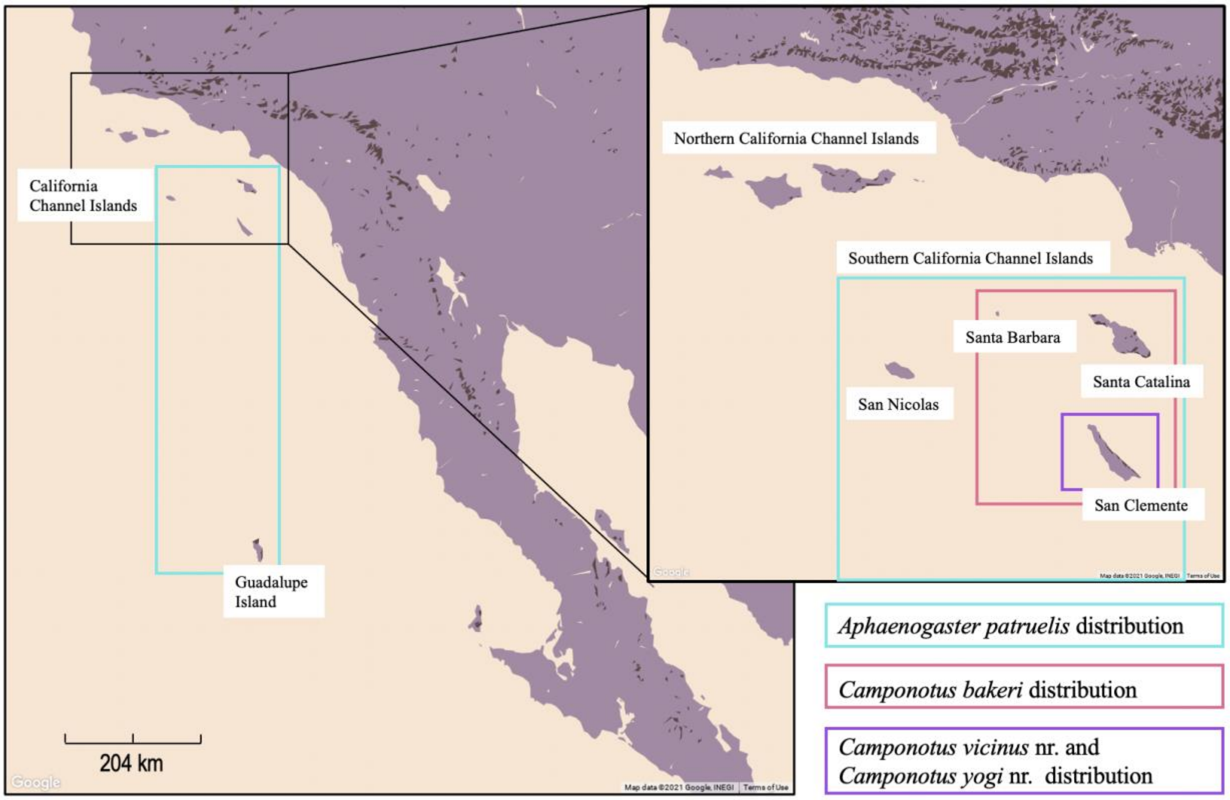
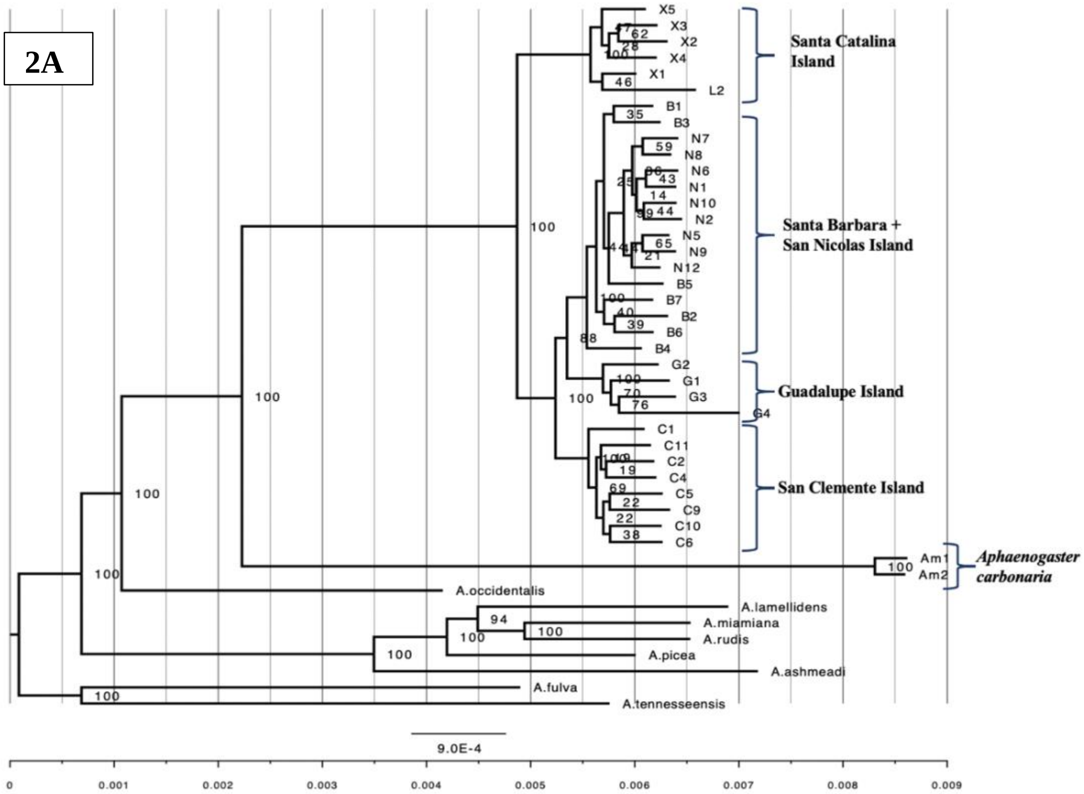
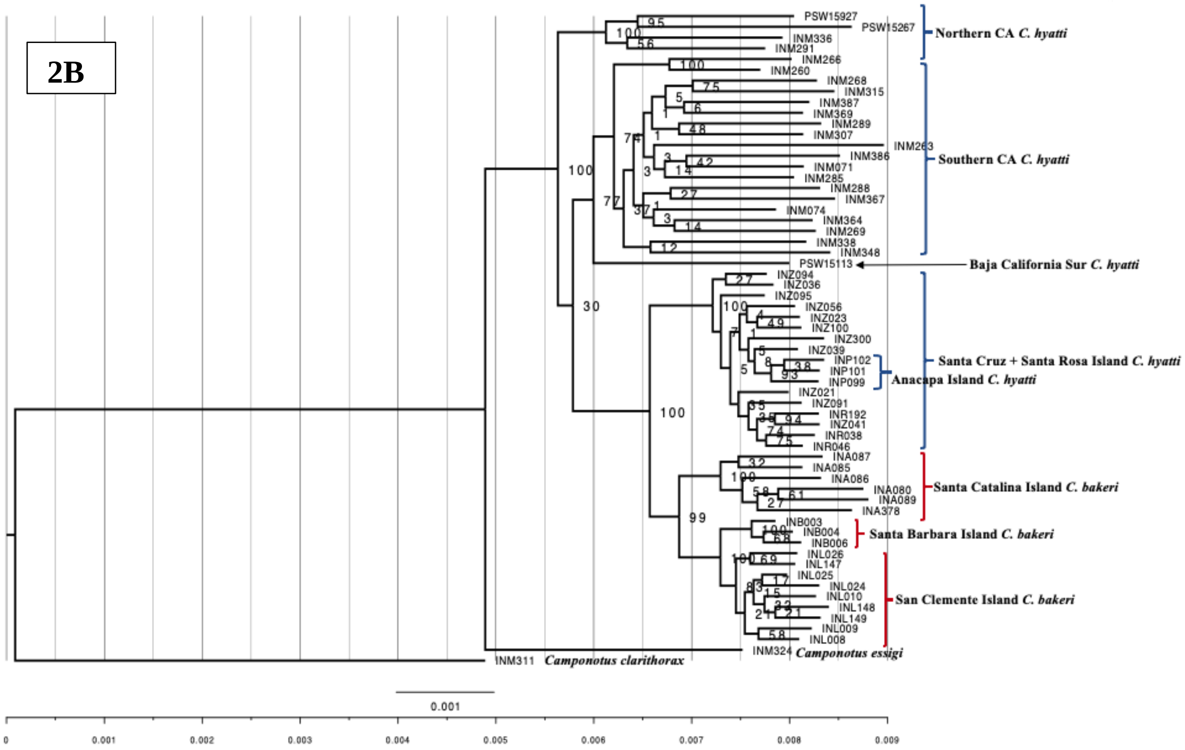


Figure 2-1. Map of the California Channel Islands and Guadalupe Island including island distributions for each endemic taxon.

Figure 2-2. RAxML maximum likelihood phylogenies for ant species endemic to the California Channel Islands: **(A)** *Aphaenogaster patruelis* **(B)** *Camponotus bakeri* / *C. hyatti* (**C)** *Camponotus vicinus* nr./ *C. vicinus* **(D)** *Camponotus yogi* nr. / *C. yogi*. Branch lengths represent average number of nucleotide substitutions per site. 1000 bootstrap replications and GTR+GAMMA substitution model used for all trees.


2A
X5
X3
X2
X4
X1
L2
Santa Catalina Island
B1
B3
N7
N8
N6
N1
N10
N2
N5
N9
N12
B5
B7
B2
B6
B4
Santa Barbara + San Nicolas Island
G2
G1
G3
G4
Guadalupe Island
C1
C11
C2
C4
C5
C9
C10
C6
San Clemente Island
Am1
Am2
Aphaenogaster carbonaria
A.occidentalis
A.lamellidens
A.miamiana
A.rudis
A.picea
A.ashmeadi
A.fulva
A.tennesseensis
100
9.0E-4
0
0.001
0.002
0.003
0.004
0.005
0.006
0.007
0.008
0.009


2B
PSW15927
PSW15267
INM336
INM291
Northern CA *C. hyatti*
INM266
INM260
INM268
INM315
INM387
INM369
INM289
INM307
INM263
INM386
INM071
INM285
INM288
INM367
INM074
INM364
INM269
INM338
INM348
Southern CA *C. hyatti*
PSW15113
Baja California Sur *C. hyatti*
INZ094
INZ036
INZ095
INZ056
INZ023
INZ100
INZ300
INZ039
INP102
INP101
INP099
Anacapa Island *C. hyatti*
INZ021
INZ091
INR192
INZ041
INR038
INR046
Santa Cruz + Santa Rosa Island *C. hyatti*
INA087
INA085
INA086
INA080
INA089
INA378
Santa Catalina Island *C. bakeri*
INB003
INB004
INB006
Santa Barbara Island *C. bakeri*
INL026
INL147
INL025
INL024
INL010
INL148
INL149
INL009
INL008
San Clemente Island *C. bakeri*
INM324 *Camponotus essigi*
INM311 *Camponotus clarithorax*
100
0.001
0
0.001
0.002
0.003
0.004
0.005
0.006
0.007
0.008
0.009

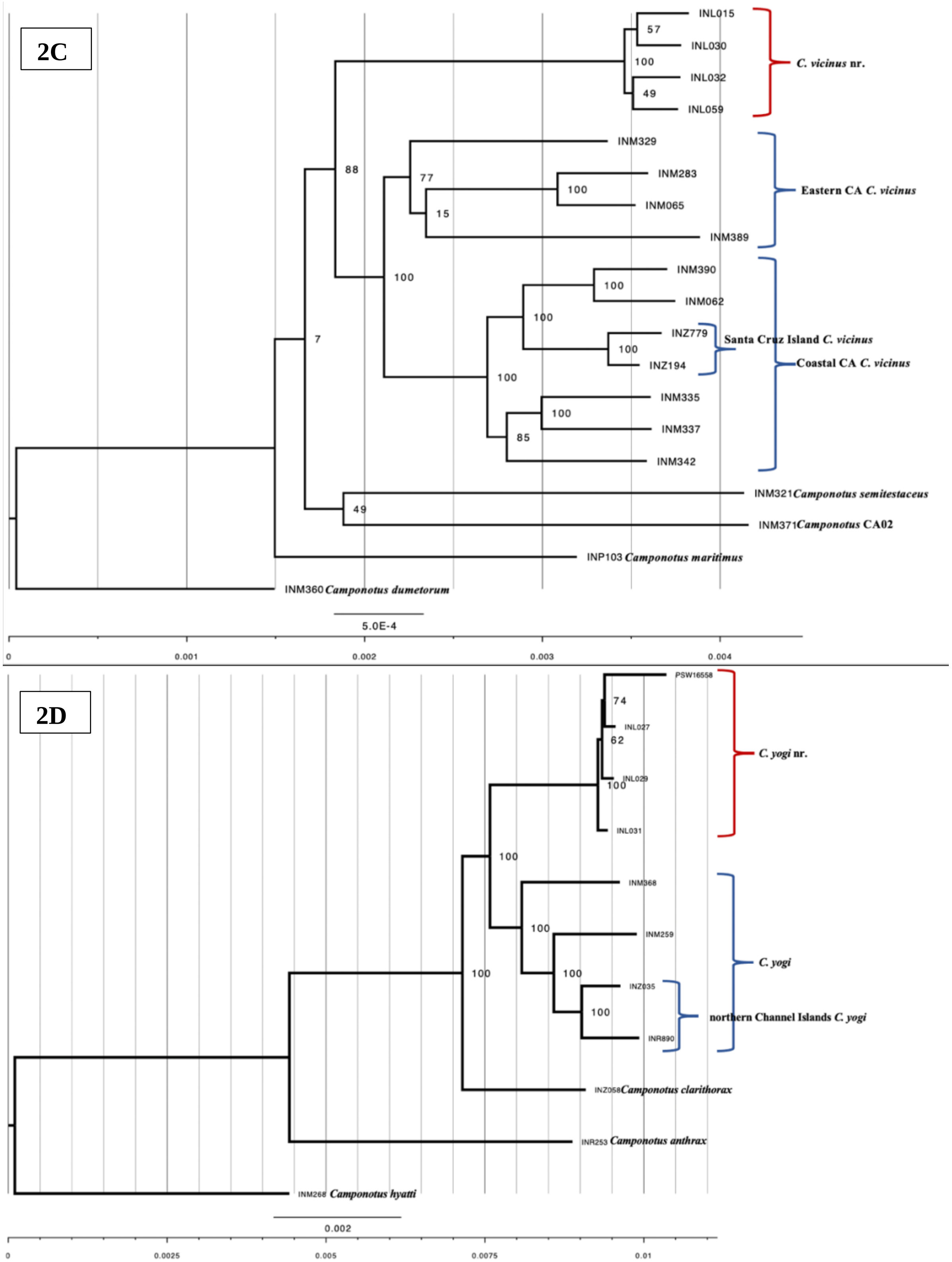
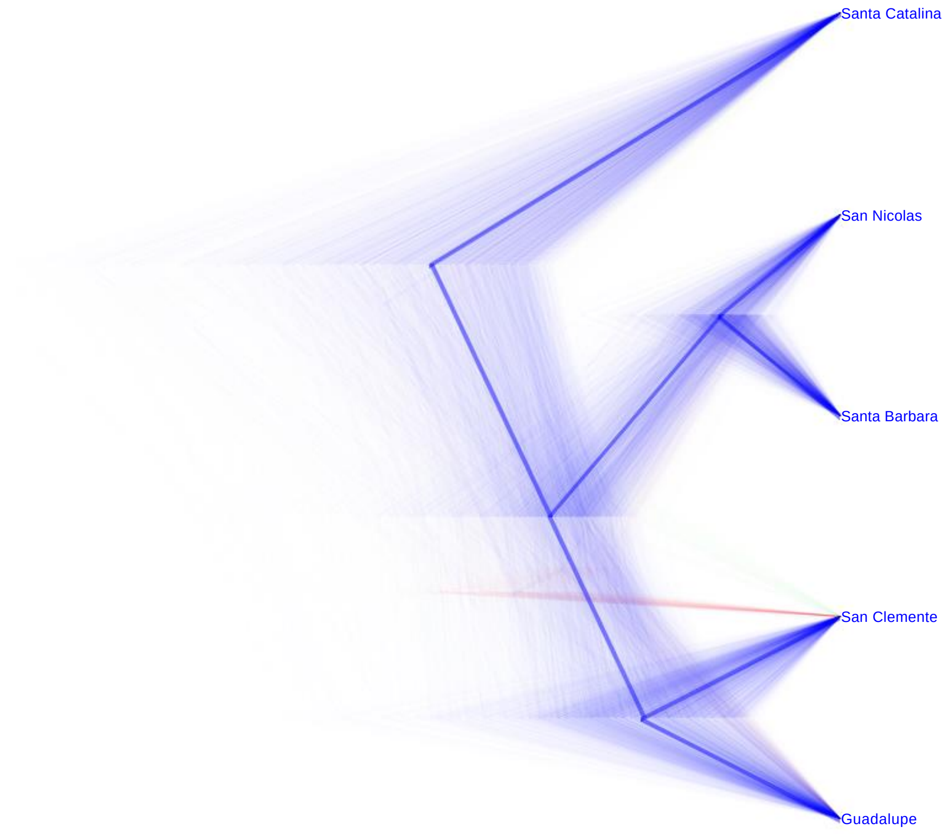
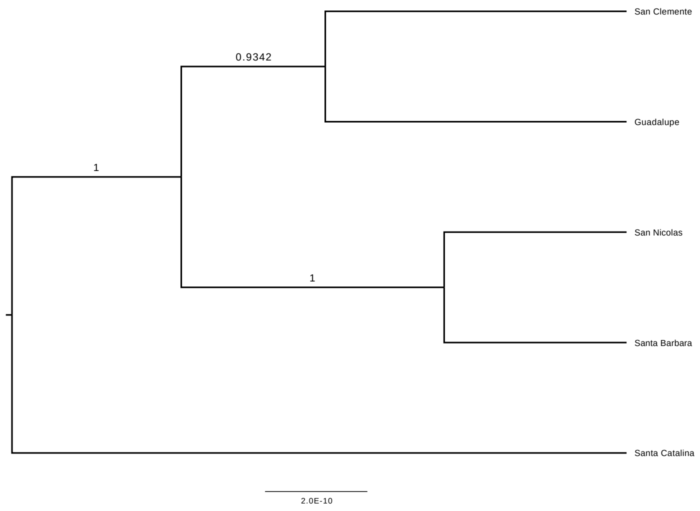


Figure 2-2. RAxML maximum likelihood phylogenies for ant species endemic to the California Channel Islands, *continued*.

Figure 2-3. SNAPP analyses based on unlinked SNP data for ant species endemic to the California Channel Islands: **(A)** *Aphaenogaster patruelis* **(B)** *Camponotus bakeri* / *C. hyatti* (**C)** *Camponotus vicinus* nr./ *C. vicinus* **(D)** *Camponotus yogi* nr. / *C. yogi*. Posterior probability for each clade is shown in the summary tree below each SNAPP tree.

3A


Santa Catalina
San Nicolas
Santa Barbara
San Clemente
Guadalupe


San Clemente
0.9342
Guadalupe
1
San Nicolas
1
Santa Barbara
Santa Catalina
2.0E-10

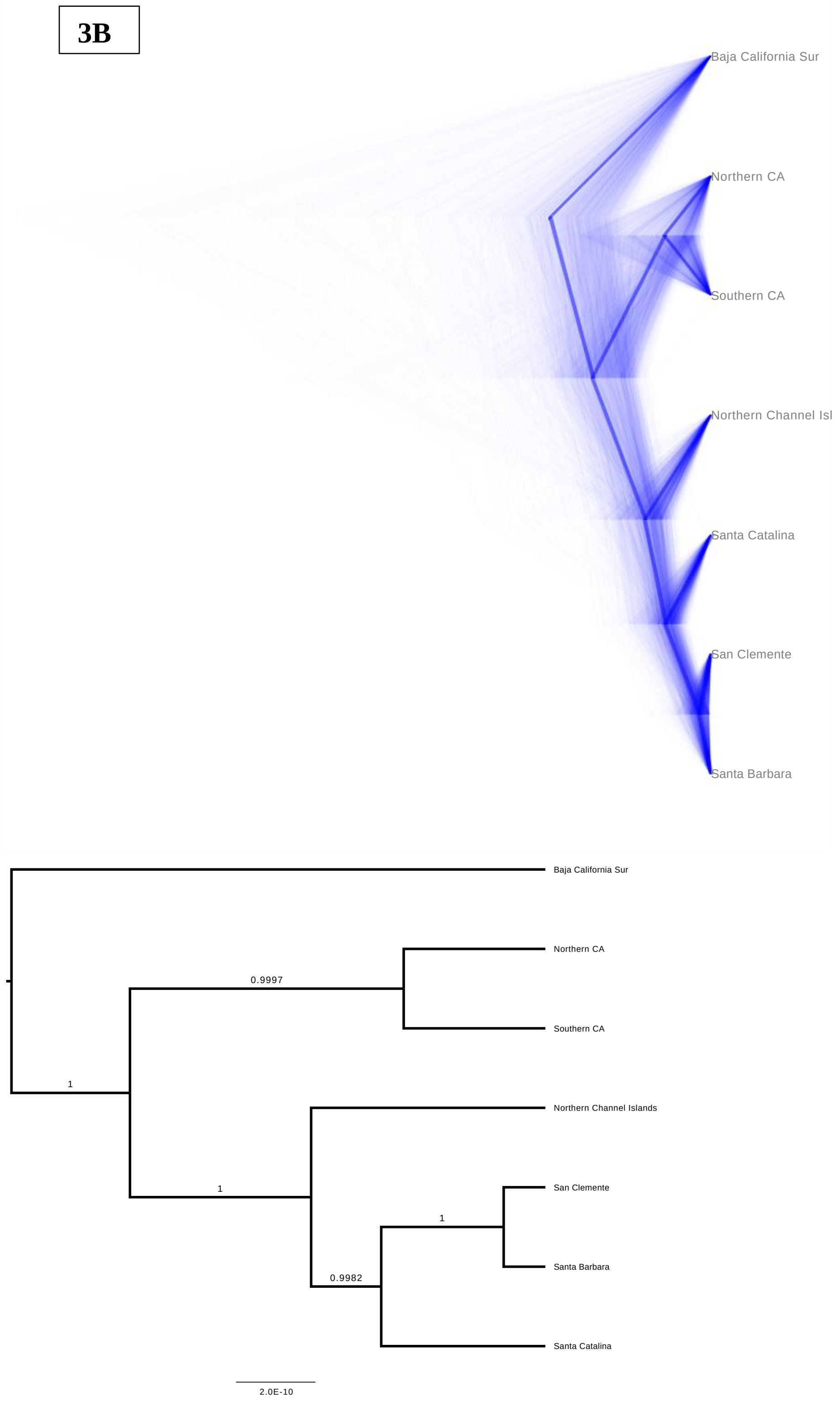


Figure 2-3. SNAPP analyses based on unlinked SNP data for ant species endemic to the California Channel Islands, *continued.*

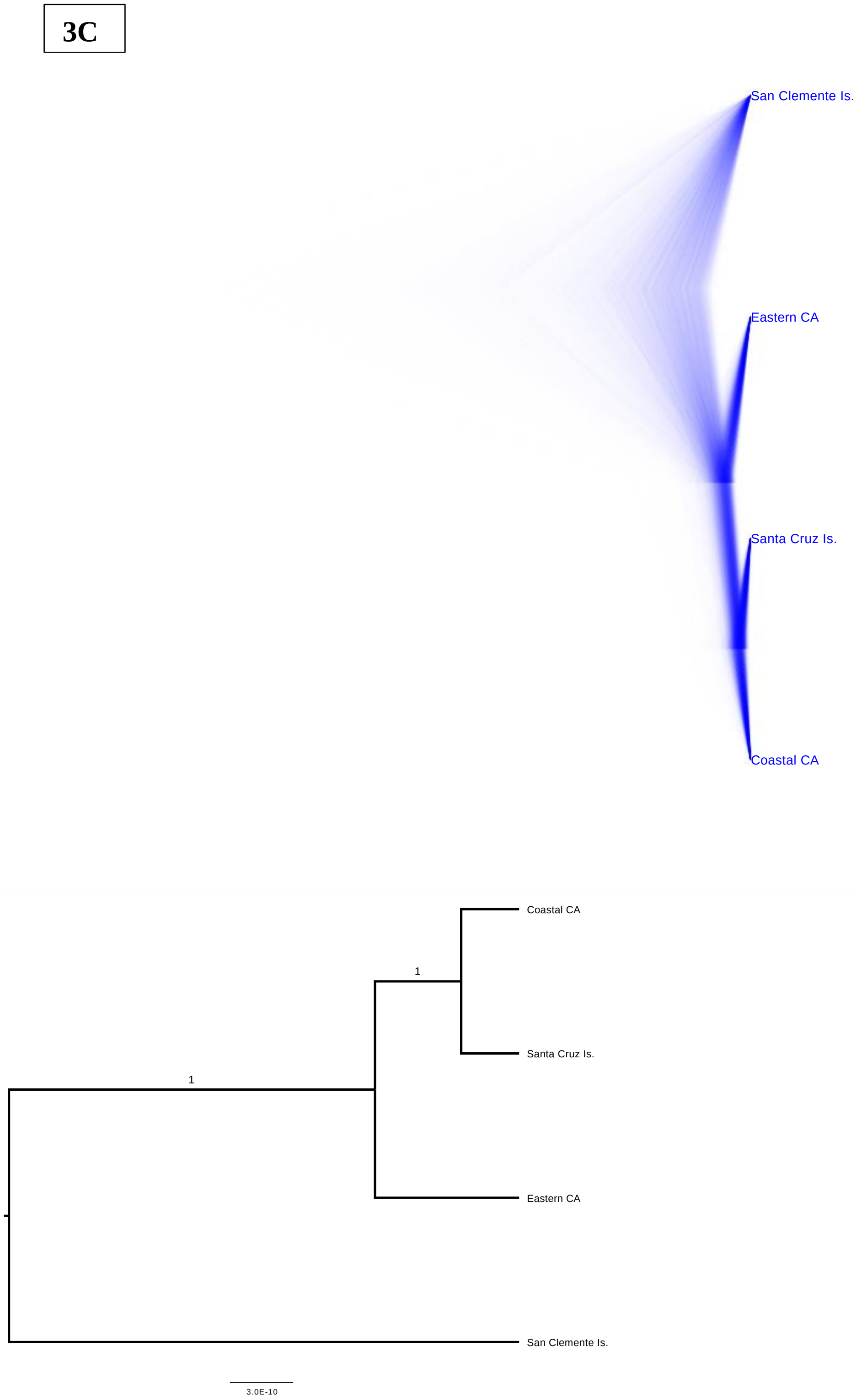


Figure 2-3. SNAPP analyses based on unlinked SNP data for ant species endemic to the California Channel Islands, *continued*

3D

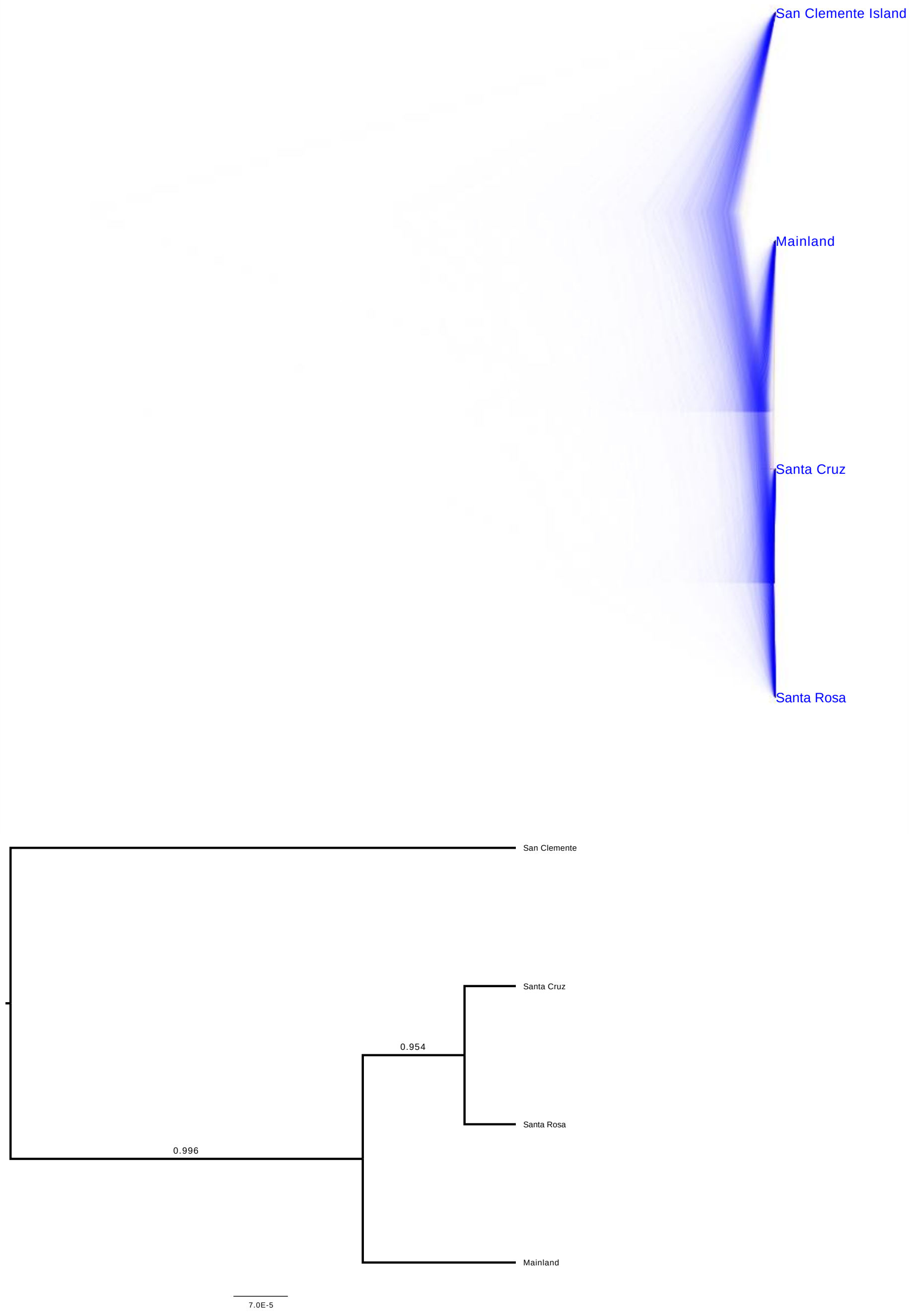
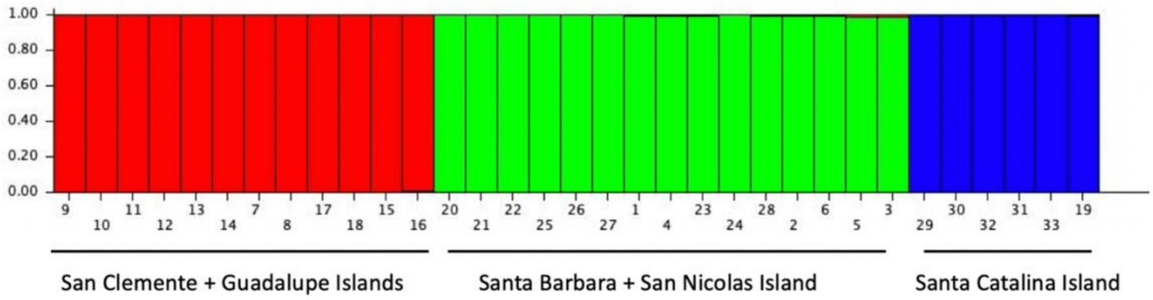


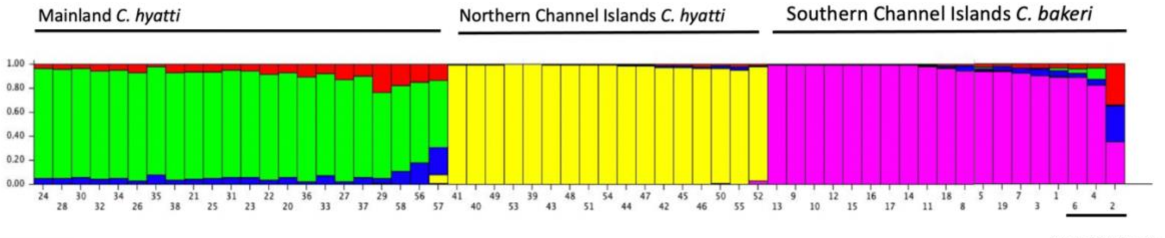
Figure 2-3. SNAPP analyses based on unlinked SNP data for ant species endemic to the California Channel Islands, *continued.*

Figure 2-4. STRUCTURE plots based on SNP data for ant species endemic to the California Channel Islands: **(A)** *Aphaenogaster patruelis* **(B)** *Camponotus bakeri* / *C. hyatti* (**C)** *Camponotus vicinus* nr./ *C. vicinus* **(D)** *Camponotus yogi* nr. / *C. yogi*. Value of K selected based on the Evanno method (Evanno et al. 2005); each column represents one sampling location. The number of SNPs and the levels of K for each species are as follows: *A. patruelis* (1874 SNPs; K = 3), *C. bakeri* / *C. hyatti* (2359 SNPs; K = 5), *C. vicinus* nr./ *C. vicinus* (928 SNPs, K = 3), *C. yogi* nr. / *C. yogi* (1781 SNPs; K = 3).

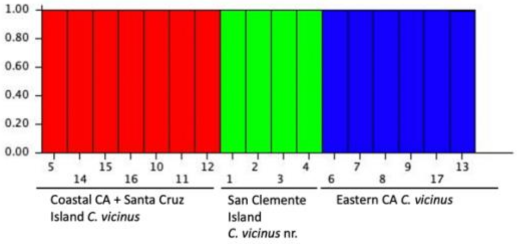
4A


1.00
0.80
0.60
0.40
0.20
0.00
9
10
11
12
13
14
7
8
17
18
15
16
20
21
22
25
26
27
1
4
23
24
28
2
6
5
3
29
30
32
31
33
19
San Clemente + Guadalupe Islands
Santa Barbara + San Nicolas Island
Santa Catalina Island

4B


Mainland *C. hyatti*
Northern Channel Islands *C. hyatti*
Southern Channel Islands *C. bakeri*
1.00
0.80
0.60
0.40
0.20
0.00
24
28
30
32
34
26
35
38
21
25
31
23
22
20
36
33
27
37
29
58
56
57
41
40
49
53
39
43
48
51
54
44
47
42
45
46
50
55
52
13
9
10
12
15
16
17
14
11
18
8
5
19
7
3
1
6
4
2
Santa Catalina Is.

4C


1.00
0.80
0.60
0.40
0.20
0.00
5
14
15
16
10
11
12
1
2
3
4
6
7
8
9
17
13
Coastal CA + Santa Cruz Island *C. vicinus*
San Clemente Island *C. vicinus* nr.
Eastern CA *C. vicinus*

4D

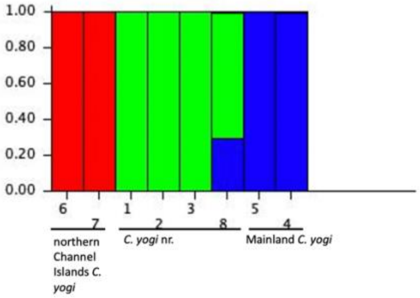

1.00
0.80
0.60
0.40
0.20
0.00
6
7
1
2
3
8
5
4
northern Channel Islands *C. yogi*
C. yogi nr.
Mainland *C. yogi*

Table 2-S1. Sample Collection Locality, Date, and Collector. Asterisks (*) denote samples included in the SNAPP analyses.

Label	Species	State	County	Island	Location	Coordinates	Date	Collector
Am1	*A. carbonaria*	Baja California	X	X	1km W La Laguna	23.55070 -109.99170	30.xii.2003	Philip S. Ward
Am2	*A. carbonaria*	Baja California	X	X	1km W La Laguna	23.55070 -109.99170	30.xii.2003	Philip S. Ward
B1	*A. patruelis*	California	Santa Barbara Co.	Santa Barbara	Middle Canyon	33.47766 -119.03080	17.vii.2014	David A. Holway
B2*	*A. patruelis*	California	Santa Barbara Co.	Santa Barbara	SW of N Peak	33.47794 -119.03794	17.vii.2014	David A. Holway
B3	*A. patruelis*	California	Santa Barbara Co.	Santa Barbara	X	33.47495 -119.03489	19.vii.2014	Ida Naughton
B4	*A. patruelis*	California	Santa Barbara Co.	Santa Barbara	Grave Yard Canyon	33.47755 -119.03019	18.vii.2014	Ida Naughton
B5	*A. patruelis*	California	Santa Barbara Co.	Santa Barbara	North Point	33.48765 -119.02935	14.vii.2014	Ida Naughton
B6*	*A. patruelis*	California	Santa Barbara Co.	Santa Barbara	Cave Canyon	33.47908 -119.03052	14.vii.2014	David A. Holway
B7	*A. patruelis*	California	Santa Barbara Co.	Santa Barbara	Under Atraplex	33.48745 -119.02993	14.vii.2014	Ida Naughton
C1	*A. patruelis*	California	Los Angeles Co.	San Clemente	Horton Canyon	32.90560 -118.47855	22.v.2016	Ida Naughton
C10	*A. patruelis*	California	Los Angeles Co.	San Clemente	Burns Canyon	32.91744 -118.48583	25.iv.2018	David A. Holway
C11	*A. patruelis*	California	Los Angeles Co.	San Clemente	Burns Canyon	32.91744 -118.48583	25.iv.2018	David A. Holway
C2*	*A. patruelis*	California	Los Angeles Co.	San Clemente	Norton Canyon	32.88306 -118.48215	21.v.2016	Ida Naughton
C4	*A. patruelis*	California	Los Angeles Co.	San Clemente	NW Wilson Cove	33.02812 -118.59116	13.iii.2015	David A. Holway
C5*	*A. patruelis*	California	Los Angeles Co.	San Clemente	Plot 7U	32.93758 -118.52897	14.iii.2016	David A. Holway
C6*	*A. patruelis*	California	Los Angeles Co.	San Clemente	Plot 7U	32.93758 -118.52897	14.iii.2015	David A. Holway
C9	*A. patruelis*	California	Los Angeles Co.	San Clemente	Plot 3I	32.96461 -118.54269	28.vii.2017	David A. Holway
G1*	*A. patruelis*	Baja California	X	Isla Gradalupe	X	29.10549 -118.31982	X	X
G2	*A. patruelis*	Baja California	X	Isla Gradalupe	X	29.10549 -118.31982	X	Christina Boser
G3*	*A. patruelis*	Baja California	X	Isla Gradalupe	X	29.10549 -118.31982	X	Christina Boser
G4	*A. patruelis*	Baja California	X	Isla Gradalupe	X	29.10549 -118.31982	X	X
N1*	*A. patruelis*	California	Ventura Co.	San Nicolas	Airfield	33.2339 -119.454331	6.vi.2016	Ida Naughton
N10	*A. patruelis*	California	Ventura Co.	San Nicolas	X	33.24458 -119.53458	4.vi.2016	David A. Holway
N12*	*A. patruelis*	California	Ventura Co.	San Nicolas	X	33.25128 -119.47023	4.vi.2016	David A. Holway
N2	*A. patruelis*	California	Ventura Co.	San Nicolas	X	33.24458 -119.53458	X	X
N5	*A. patruelis*	California	Ventura Co.	San Nicolas	Grand Canyon	33.23486 -119.52177	14.ix.2017	Ida Naughton
N6	*A. patruelis*	California	Ventura Co.	San Nicolas	Rock Crusher	33.25997 -119.57202	12.ix.2017	David A. Holway
N7	*A. patruelis*	California	Ventura Co.	San Nicolas	X	33.23555 -119.44156	v.vi.2016	David A. Holway
N8	*A. patruelis*	California	Ventura Co.	San Nicolas	X	33.25333 -119.50046	3.vi.2016	David A. Holway
N9	*A. patruelis*	California	Ventura Co.	San Nicolas	X	33.24158 -119.47363	3.vi.2016	David A. Holway
X1*	*A. patruelis*	California	Los Angeles Co.	Santa Catalina	X	33.35108 -118.35285	22.v.2018	David A. Holway
X2	*A. patruelis*	California	Los Angeles Co.	Santa Catalina	X	33.41011 -118.46688	22.v.2018	David A. Holway
X3*	*A. patruelis*	California	Los Angeles Co.	Santa Catalina	X	33.41011 -118.46688	22.v.2018	David A. Holway
X4	*A. patruelis*	California	Los Angeles Co.	Santa Catalina	X	33.35338 -118.39660	22.v.2018	David A. Holway
X5*	*A. patruelis*	California	Los Angeles Co.	Santa Catalina	X	33.35338 -118.39660	22.v.2018	David A. Holway
X10	*A. patruelis*	California	Los Angeles Co.	Santa Catalina	Middle Canyon, Johnson Tree	33.38740 -118.39540	8.vi.2015	David A. Holway
A113	A. *miamiana*	Mississippi	Oktibeha Co.	X	Osborne Prairie	33.51471 -88.73166	8.iii.2010	Bernice B. DeMarco
A142	*A. tennesseensis*	Minnesota	Olmsted Co.	X	Quarry Hill Nature Center	44.05983 -92.48716	11.vii.2010	Bernice B. DeMarco
A209	*A. fulva*	Virginia	Surry Co.	X	York River State Park	37.40945 -76.71361	12.viii.2010	Bernice B. DeMarco
A282	*A. ashmeadi*	North Carolina	Bladen Co.	X	Culbreth Smith & Lula Loop Rd	34.75881 -78.58973	27.vii.2010	Bernice B. DeMarco
A295	*A. lamellidens*	North Carolina	Orange Co.	X	Duke Forest Warming Project	36.03643 -79.07746	28.vii.2011	Bernice B. DeMarco
A30	A. *picea*	Michigan	Ingham Co.	X	Rose Lake	42.80040 -84.38158	31.v.2010	Bernice B. DeMarco
Ar	*A. rudis*	New Jersey	Middlesex Co.	X	Cheesequake State Park	40.43805 -74.26000	30.v.2010	Bernice B. DeMarco
N4	*A. occidentalis*	California	Marin Co.	X	Marin Headlands	37.82822 -122.49752	4.vii.2012	Ida Naughton
Na	*N. albisetosus*	Arizona	Cochise Co.	X	Chiricahua Mts SWRS 7kmW	31.88333 -109.20000	8.viii.2009	Bernice B. DeMarco
Nc	*N. cockerelli*	Arizona	Cochise Co.	X	Chiricahua Mts SWRS 7kmW	31.88333 -109.20000	8.viii.2009	Bernice B. DeMarco
L2	*A. patruelis*	California	Los Angeles Co.	Santa Catalina	X	X	8/3/2007	X
INA085*	*C. bakeri*	California	Los Angeles Co.	Santa Catalina	Airport rd.	33.34847 -118.35194	9.vi.2015	David A. Holway
INA086*	*C. bakeri*	California	Los Angeles Co.	Santa Catalina	Airport rd. upper cape reserve	33.35722 -118.36402	9.vi.2015	David A. Holway
INA087	*C. bakeri*	California	Los Angeles Co.	Santa Catalina	Airport rd. empire landing	33.36082 -118.36960	9.vi.2015	David A. Holway
INA089	*C. bakeri*	California	Los Angeles Co.	Santa Catalina	Upper cape canyon	33.36082 -118.36960	9.vi.2015	David A. Holway
INB003*	*C. bakeri*	California	Ventura Co.	Santa Barbara		33.48016 -119.03401	19.vii.2014	Ida Naughton
INB004	*C. bakeri*	California	Ventura Co.	Santa Barbara		33.48024 -119.04027	17.vii.2014	Ida Naughton
INB006*	*C. bakeri*	California	Ventura Co.	Santa Barbara		33.47372 -119.03477	19.vii.2014	Ida Naughton
INL008*	*C. bakeri*	California	Los Angeles Co.	San Clemente	Signal Peak	32.90468 -118.49629	30.viii.2013	David A. Holway
INL009	*C. bakeri*	California	Los Angeles Co.	San Clemente	9U Wilson's Cove	32.99512 -118.55169	23.viii.2014	David A. Holway
INL010	*C. bakeri*	California	Los Angeles Co.	San Clemente	Wilson Cove	32.99407 -118.55330	23.viii.2014	Ida Naughton
INL024	*C. bakeri*	California	Los Angeles Co.	San Clemente	Flasher Dunes	32.99846 -118.57884	15.iii.2015	Ida Naughton
INL025	*C. bakeri*	California	Los Angeles Co.	San Clemente	West Cove	33.01630 -118.59577	16.iii.2015	Ida Naughton
INL026*	*C. bakeri*	California	Los Angeles Co.	San Clemente	West Cove	33.01579 -118.59498	13.iii.2015	Ida Naughton
INA378	*C. bakeri*	California	Los Angeles Co.	Santa Catalina	USGS #10	X	X	X
INL147	*C. bakeri*	California	Los Angeles Co.	San Clemente	West Cove	33.01695 -118.59742	20.v.2016	Ida Naughton
INL148	*C. bakeri*	California	Los Angeles Co.	San Clemente	Flasher Dunes	32.99328 -118.57644	22.v.2016	Ida Naughton
INL149	*C. bakeri*	California	Los Angeles Co.	San Clemente		32.99028 -118.57188	22.v.2016	Ida Naughton
INA080	*C. bakeri*	California	Los Angeles Co.	Santa Catalina	Blackjack junction	33.36082 -118.36960	9.vi.2015	David A. Holway
INM071	*C. hyatti*	California	San Diego Co.	Mainland	Mount Laguna	32.81778 -116.4478	14.ii.2014	Ida Naughton
INM074	*C. hyatti*	California	San Diego Co.	Mainland	Mount Laguna	32.81778 -116.4478	14.ii.2014	Ida Naughton
INP099	*C. hyatti*	California	Santa Barbara Co.	Anacapa	West, Oak canyon	34.00343 -120.05310	15.ix.2015	Ida Naughton
INP101	*C. hyatti*	California	Santa Barbara Co.	Anacapa	West, Oak canyon	34.00343 -120.05310	15.ix.2015	Ida Naughton
INP102*	*C. hyatti*	California	Santa Barbara Co.	Anacapa	West, Oak canyon	34.00343 -120.05310	15.ix.2015	Ida Naughton

INR038	*C. hyatti*	California	Santa Barbara Co.	Santa Rosa		33.95445 -119.98735	22.iv.2015	Ida Naughton
INR046*	*C. hyatti*	California	Santa Barbara Co.	Santa Rosa		34.00343 -120.05310	24.iv.2015	Ida Naughton
INR192*	*C. hyatti*	California	Santa Barbara Co.	Santa Rosa		33.95445 -119.98735	23.iv.2015	Ida Naughton
INZ021	*C. hyatti*	California	Santa Barbara Co.	Santa Cruz	2U	33.99335 -119.69445	vi.10.2014	Ida Naughton
INZ023	*C. hyatti*	California	Santa Barbara Co.	Santa Cruz	1U	33.99882 -119.72769	vi.10.2014	Ida Naughton
INZ036	*C. hyatti*	California	Santa Barbara Co.	Santa Cruz	9U	34.00100 -119.73572	vi.10.2014	Ida Naughton
INZ039	*C. hyatti*	California	Santa Barbara Co.	Santa Rosa		33.98815 -120.07318	23.4.2015	Ida Naughton
INZ041	*C. hyatti*	California	Santa Barbara Co.	Santa Cruz		34.00190 -119.74006	23.vi.2015	Ida Naughton
INZ056	*C. hyatti*	California	Santa Barbara Co.	Santa Cruz	Cueva Valdez	34.05341 -119.76578	29.vi.2015	Ida Naughton
INZ091	*C. hyatti*	California	Santa Barbara Co.	Santa Cruz	Christi Ranch	34.05095 -119.81598	1.vi.2014	Ida Naughton
INZ094	*C. hyatti*	California	Santa Barbara Co.	Santa Cruz		34.05095 -119.81598	2.vi.2014	Ida Naughton
INZ095	*C. hyatti*	California	Santa Barbara Co.	Santa Cruz	Isthmus	34.00107 -119.64367	4.iv.2014	Ida Naughton
INZ100	*C. hyatti*	California	Santa Barbara Co.	Santa Cruz	Cueva Valdez	33.98993 -119.67665	29.vi.2015	Ida Naughton
INZ300	*C. hyatti*	California	Santa Barbara Co.	Santa Cruz	China Pines	34.00275 -119.61715	31.v.2017	Ida Naughton
INM260	*C. hyatti*	California	Santa Barbara Co.	Mainland	Sedgwick	34.74050 -120.05659	17.iv.2018	Ida Naughton
INM263	*C. hyatti*	California	Santa Barbara Co.	Mainland	Sedgwick	34.69143 -120.04161	17.iv.2018	Ida Naughton
INM266	*C. hyatti*	California	Santa Barbara Co.	Mainland	Figueroa Mtn.	34.74049 -120.05678	18.iv.2018	Ida Naughton
INM268	*C. hyatti*	California	Santa Barbara Co.	Mainland	Santa Ynez	34.65528 -120.06022	18.iv.2018	Ida Naughton
INM269	*C. hyatti*	California	Santa Barbara Co.	Mainland	East Camino Cielo	34.51923 -119.79806	18.iv.2018	Ida Naughton
INM285	*C. hyatti*	California	Riverside Co.	Mainland	James San Jacinto	33.80890 -116.77544	25.iv.2018	Ida Naughton
INM288	*C. hyatti*	California	San Bernardino co.	Mainland	HWY 330	34.19118 -117.15498	27.iv.2018	Ida Naughton
INM289	*C. hyatti*	California	Los Angeles Co.	Mainland	HWY 2	34.27367 -118.03219	27.iv.2018	Ida Naughton
INM291*	*C. hyatti*	California	Kern Co.	Mainland	Owen's Pass	35.66507 -118.03625	29.iv.2018	Ida Naughton
INM315*	*C. hyatti*	California	Los Angeles Co.	Mainland	Santa Monica Mountains	34.09858 -118.30235	30.iv.2018	Ida Naughton
INM348	*C. hyatti*	California	San Mateo Co.	Mainland	Thornewood Preserve	37.35542 -122.17242	3.vi.2018	Ida Naughton
INM364*	*C. hyatti*	California	San Diego Co.	Mainland	Buckman Springs	32.76094 -116.48192	28.v.2018	Ida Naughton
INM367	*C. hyatti*	California	San Diego Co.	Mainland	Lyon's Valley	32.72992 -116.69427	28.v.2018	Ida Naughton
INM369	*C. hyatti*	California	San Diego Co.	Mainland	Alpine	32.76015 -116.67396	28.v.2018	Ida Naughton
INM307	*C. hyatti*	California	Los Angeles Co.	Mainland	Stunt Ranch Reserve	34.09858 -118.30235	30.iv.2018	Ida Naughton
INM336*	*C. hyatti*	California	Marin Co.	Mainland	Muir Woods	37.88070 -122.58083	2.vi.2018	Ida Naughton
INM338	*C. hyatti*	California	San Mateo Co.	Mainland	La Honda Rd.	37.39563 -122.25626	3.vi.2018	Ida Naughton
INM386	*C. hyatti*	California	Riverside Co.	Mainland	Tenaja Truck Trail	33.53299 -117.39324	12.vi.2018	David A. Holway
INM387	*C. hyatti*	California	Riverside Co.	Mainland	Clinton Keith Road	33.55891 -117.26426	12.vi.2018	David A. Holway
INM324	*C. essigi*	California	Yolo Co.	Mainland	McLaughlin Reserve	38.86834 -122.42064	1.v.2018	Ida Naughton
INM311	*C. clarithorax*	California	Los Angeles Co.	Mainland	Stunt Ranch Reserve	34.09404 -118.65608	30.iv.2018	Ida Naughton
PSW15267	*C. hyatti*	California	Lassen Co.	Mainland	Hallelujah Junction	39.7746 -120.07083	2.vii.2004	Philip S. Ward
PSW15927	*C. hyatti*	California	Modoc Co.	Mainland	ENE Cedarville	41.58438 -120.03207	21.vi.2007	Philip S. Ward
PSW15113*	*C. hyatti*	Baja California Sur		Mainland	W La Laguna	23.55070 -109.99170	30.12.2003	Philip S. Ward
INM368*	*C. yogi*	California	San Diego	Mainland	Campo	32.62275 -116.75709	28.v.18	Ida Naughton
INM259*	*C. yogi*	California	Santa Barbara Co.	Mainland	Sedgwick	34.69143 -120.04161	17.iv.2018	Ida Naughton
INZ035*	*C. yogi*	California	Santa Barbara Co.	Santa Cruz Island	Central Valley	34.00479 -119.75004	21.3.2015	Ida Naughton
INL031*	*C. yogi* nr.	California	Los Angeles Co.	San Clemente	Flasher Dunes	32.99630 -118.57937	16.iii.2015	Ida Naughton
INL029	*C. yogi* nr.	California	Los Angeles Co.	San Clemente	Flasher Dunes	32.99448 -118.57641	15.iii.2015	Ida Naughton
PSW16558	*C. yogi* nr.	California	Los Angeles Co.	San Clemente	West Cove	33.01442 -118.59452	25.iii.2011	Philip S. Ward
INL027*	*C. yogi* nr.	California	Los Angeles Co.	San Clemente	Flasher Dunes	32.99122 -118.57626	15.iii.2015	Ida Naughton
INR890*	*C. yogi*	California	Santa Barbara Co.	Santa Rosa	Black Mountain	33.98065 -120.07258	14.vii.2019	Ida Naughton
INZ058	*C. clarithorax*	California	Santa Barbara Co.	Santa Cruz	Bishop Pines	34.00972 -119.80658	2.vi.2017	Ida Naughton
INR253	*C. anthrax*	California	Santa Barbara Co.	Santa Rosa	Cherry Canyon	34.00026 -120.05718	8.iv.2017	Ida Naughton
INZ194*	*C. vicinus*	California	Santa Barbara Co.	Santa Cruz	China Pines	34.00275 -119.61715	31.v.2017	Ida Naughton
INM342*	*C. vicinus*	California	San Mateo Co.	Mainland	Thornewood Preserve	37.39863 -122.25626	3.vi.2018	Ida Naughton
INM335	*C. vicinus*	California	Marin Co.	Mainland	Muir Woods	37.88015 -122.58121	2.vi.2018	Ida Naughton
INM062	*C. vicinus*	California	Santa Barbara Co.	Mainland	Vandenberg Air Force Base	34.74626 -120.61813	26.viii.2018	Ida Naughton
INM389*	*C. vicinus*	Arizona	Kayenta Co.	Mainland		36.67195 -110.55798	16.ix.2017	Ida Naughton
INM292*	*C. vicinus*	California	Kern Co.	Mainland	Owen's Pass	35.66581 -118.03565	29.iv.2018	Ida Naughton
INM065*	*C. vicinus*	California	Riverside Co.	Mainland	Palomar Mtn.	33.33652 -116.89368	11.xi.2014	Ida Naughton
INM283*	*C. vicinus*	California	Riverside Co.	Mainland	James San Jacinto	33.80710 -116.77431	25.iv.2018	Ida Naughton
INL015*	*C. vicinus* nr.	California	Los Angeles Co.	San Clemente	Wilson Cove	32.99666 -118.56087	21.ii.2014	Ida Naughton
INL030	*C. vicinus* nr.	California	Los Angeles Co.	San Clemente	REWS Cyn.	32.91369 -118.52747	14.3.2015	Ida Naughton
INL059*	*C. vicinus* nr.	California	Los Angeles Co.	San Clemente	Boulder Cyn.	32.89384 -118.49659	11.vii.2015	Ida Naughton
INL032	*C. vicinus* nr.	California	Los Angeles Co.	San Clemente	Boulder Cyn.	32.89069 -118.50175	11.vii.2015	Ida Naughton
INM329*	*C. vicinus*	California	Yolo Co.	Mainland	McLaughlin Reserve	38.86834 -122.42064	2.v.2018	Ida Naughton
INM337*	*C. vicinus*	California	Marin Co.	Mainland	Muir Woods	37.87956 -122.58048	30.iv.2018	Ida Naughton
INM390	*C. vicinus*	California	Santa Barbara Co.	Mainland	Lompoc	34.72618 -120.46566	4.v.2015	Ida Naughton
INZ779*	*C. vicinus*	California	Santa Barbara Co.	Santa Cruz	Montañon	34.01006 -119.59245	14.iv.2019	Ida Naughton
INM326	*C. semitestaceus*	California	Yolo Co.	Mainland	McLaughlin Reserve	38.86834 -122.42064	1.v.2018	Ida Naughton
INP103	*C. maritimus*	California	Santa Barbara Co.	Anacapa	Oak Canyon	34.01182 -119.42448	15.ix.2015	Ida Naughton
INM360	*C. dumetorum*	California	San Diego Co.	Mainland	Black Mountain	32.98909 -117.12219	14.vi.2018	Ida Naughton

Table 2-S2. Trimmed read count metrics for Illumina HiSeq 4000 data.

Sample ID	number of reads	total bp	mean length	95 CI length	minimum length	maximum length
Am1	3610971	520403844	144.1174255	0.010844624	40	151
Am2	2359248	340613726	144.3738539	0.013293774	40	151
B2	2407277	342578901	142.3097138	0.014964985	40	151
B3	1536021	213668436	139.1051529	0.021775779	40	151
B4	316005	43099556	136.3888419	0.053357453	40	151
B5	4386132	635737708	144.9426757	0.009273585	40	151
B6	3260261	462602611	141.8912814	0.013101522	40	151
B7	5336714	763125770	142.9954406	0.009672138	40	151
C1	829469	116302231	140.2128723	0.028238205	40	151
C10	3825341	554294849	144.9007681	0.01000143	40	151
C11	8259132	1187802599	143.8168804	0.007332397	40	151
C2	4065464	586003586	144.1418706	0.010277127	40	151
C4	4589139	662339778	144.3276785	0.009518943	40	151
C5	2095540	300672925	143.4823124	0.014877002	40	151
C6	3539858	508419103	143.6269768	0.011300162	40	151
C9	4730524	688803561	145.6083007	0.008434462	40	151
G1	4798558	689360658	143.6599616	0.009830074	40	151
G2	4158940	601532615	144.6360407	0.009807441	40	151
G3	4187238	602993469	144.0074505	0.010232155	40	151
G4	2803231	400970250	143.0386044	0.013322824	40	151
N1	3597259	509960218	141.7635533	0.012579185	40	151
N10	2746893	395119547	143.842351	0.012845325	40	151
N12	3346698	475590856	142.107491	0.012876336	40	151
N2	4599199	667369267	145.1055427	0.00893674	40	151
N5	4700766	680924817	144.8540125	0.009066222	40	151
N6	4736316	669785892	141.4149504	0.011138113	40	151
N7	3299483	474377479	143.7732757	0.011692367	40	151
N8	3202528	459921317	143.6119581	0.011991033	40	151
N9	4489635	647385121	144.1954905	0.009720742	40	151
X1	3039785	438440358	144.2340027	0.011714146	40	151
X2	2597752	372661994	143.45557	0.013320784	40	151
X3	3594448	522228003	145.2873996	0.009941068	40	151
X4	1884046	271614638	144.1656085	0.014949305	40	151
X5	3541577	513608113	145.0224329	0.010262025	40	151
A113	2415216	345975938	143.2484457	0.014056259	40	151
A142	2835135	410245361	144.7004679	0.011785158	40	151
A209	2097068	301140973	143.6009576	0.014876546	40	151
A282	3350965	487994072	145.6279227	0.010036911	40	151
A295	2954605	427682284	144.7510865	0.011444675	40	151
A30	2755892	395572713	143.5370882	0.012931624	40	151
Ar	3090143	449464555	145.4510536	0.010638709	40	151
N4	3331020	484361536	145.4093749	0.010289623	40	151
Na	9414996	1355032571	143.9227984	0.006819504	40	151
Nc	3736581	536265610	143.5177265	0.011066477	40	151
L2	5658736	819818456	144.8766042	0.00820388	40	151
INA085	4460462	652454792	146.2751598	0.00807083	40	151
INA086	7848618	1118933462	142.5643931	0.008094359	40	151
INA087	6236543	909020422	145.7571	0.007196149	40	151
INA089	6147191	873857050	142.1555065	0.00939093	40	151
INB003	3363266	488984063	145.3896489	0.010178167	40	151
INB004	4517578	656456989	145.3117111	0.008814117	40	151
INB006	3724545	541777464	145.4613823	0.00938807	40	151
INL008	2667936	386545849	144.8857278	0.011924778	40	151
INL009	3391465	495460371	146.0903683	0.009480012	40	151
INL010	5364320	780500212	145.4984438	0.007993574	40	151
INL024	7753998	1132995431	146.117581	0.006245323	40	151
INL025	9280627	1342035033	144.6060738	0.006535839	40	151
INL026	6035801	885641235	146.731351	0.006597967	40	151
INA378	3945916	571321874	144.7881491	0.009921644	40	151
INL147	6571063	961623284	146.3421191	0.006615477	40	151
INL148	3091417	439229001	142.0801532	0.01332969	40	151
INL149	1229323	175535422	142.7903179	0.020194381	40	151
INA080	16123965	2299676620	142.6247589	0.005615661	40	151
INM071	7867534	1110608454	141.1634769	0.00920718	40	151
INM074	12539587	1828098250	145.7861611	0.005070549	40	151
INP099	6281068	904440021	143.9946234	0.008270914	40	151
INP101	4765267	685481848	143.8496202	0.009632247	40	151
INP102	7449917	1061882947	142.5362117	0.008335131	40	151
INR038	5711087	824349116	144.3418943	0.008493325	40	151
INR046	16319167	2327783425	142.6410689	0.005577235	40	151
INR192	5328929	768951840	144.2976328	0.008814963	40	151
INZ021	11383049	1654199610	145.3213115	0.005553232	40	151
INZ023	3580936	513491054	143.3957641	0.011434316	40	151
INZ036	2431618	353273147	145.28316	0.011984598	40	151

Sample ID	number of reads	total bp	mean length	95 CI length	minimum length	maximum length
INZ039	5302274	775171182	146.1959872	0.007478896	40	151
INZ041	16267554	2325711363	142.9662605	0.005495667	40	151
INZ056	2344063	341104760	145.5185974	0.012100219	40	151
INZ091	7028973	1005719162	143.0819498	0.008302678	40	151
INZ094	5689643	808042925	142.0199694	0.009826092	40	151
INZ095	7218832	1053873259	145.9894425	0.00654034	40	151
INZ100	4574331	664827374	145.3387116	0.008578812	40	151
INZ300	2001116	289936953	144.8876292	0.013872011	40	151
INM260	2750911	396359971	144.0831677	0.012520053	40	151
INM266	3934577	570216553	144.9244869	0.009838906	40	151
INM268	2624613	381863571	145.4932864	0.011462426	40	151
INM269	2133547	308356546	144.5276556	0.013801226	40	151
INM285	4319170	625885085	144.908648	0.009406326	40	151
INM288	2714070	393453291	144.9679968	0.011806103	40	151
INM289	2506076	362468711	144.6359612	0.012577027	40	151
INM291	2183812	315514124	144.4786108	0.013677581	40	151
INM315	1864825	271181983	145.4195343	0.013679086	40	151
INM348	1324700	191909045	144.8698158	0.016987308	40	151
INM364	3255005	469146204	144.1307169	0.011444194	40	151
INM367	2422682	350741569	144.7740847	0.012691451	40	151
INM369	2727915	394715789	144.695047	0.012043018	40	151
INM307	3500353	504832647	144.2233532	0.011002357	40	151
INM336	2136956	309370498	144.7715807	0.013521042	40	151
INM338	2547847	368557248	144.6543878	0.012515358	40	151
INM386	978180	140719317	143.8583052	0.021324375	40	151
INM387	5932040	858306434	144.6899269	0.00809415	40	151
INM324	2044277	294834513	144.2243458	0.014654772	40	151
INM311	2880637	418282652	145.2049154	0.011208565	40	151
PSW15267	2575736	378497069	146.9471518	0.009858568	40	151
PSW15927	2800533	412350653	147.2400622	0.009119887	40	151
PSW15113	6614529	968262078	146.3841308	0.006560471	40	151
INM368	4334587	621805868	143.45216	0.0103836	40	151
INM259	4606859	670750188	145.5981587	0.008522255	40	151
INZ035	4034511	587176808	145.5385319	0.009136067	40	151
INL031	4282931	627792549	146.5801221	0.007998482	40	151
INL029	8356869	1221352225	146.1494999	0.006000122	40	151
PSW16558	4213166	619356772	147.0050722	0.007667987	40	151
INL027	9844801	1442777753	146.5522516	0.005306039	40	151
INR890	5340995	791389410	148.1726551	0.00606586	40	151
INZ058	5997264	876350850	146.125108	0.007098686	40	151
INR253	7382122	1067753390	144.6404421	0.007367048	40	151
INZ194	9010075	1295566749	143.7908951	0.006847263	40	151
INM342	2742044	397838157	145.088174	0.01161584	40	151
INM335	2472361	357561424	144.6234688	0.012712961	40	151
INM062	9228481	1342662952	145.4912192	0.006068699	40	151
INM389	4269638	620151840	145.2469366	0.00917136	40	151
INM292	6578387	955183983	145.200333	0.007432922	40	151
INM065	5739599	834683035	145.4253224	0.007761106	40	151
INM283	5185755	751462546	144.9089951	0.008570597	40	151
INL015	6112378	886437449	145.0233361	0.007732603	40	151
INL030	4762323	696879853	146.3319168	0.007772703	40	151
INL059	15544424	2238442690	144.0029357	0.005259006	40	151
INL032	5216115	760828308	145.861107	0.007809487	40	151
INM329	4839521	703267756	145.317637	0.008552819	40	151
INM337	5286036	769213403	145.5180031	0.008058187	40	151
INM390	1873130	271439315	144.9121604	0.014230123	40	151
INZ779	16658487	2476492910	148.6625352	0.003120937	40	151
INM326	1627333	235095818	144.4669395	0.015882408	40	151
INP103	5338593	782089515	146.4973102	0.007238966	40	151
INM360	4691656	678438919	144.605427	0.009242714	40	151

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CHAPTER 3 : A multi-species comparison of genetic diversity between island and mainland ant populations

ABSTRACT

Island populations provide unparalleled opportunities to examine evolutionary processes. Founder effects and bottlenecks, for example, typically decrease genetic diversity in island populations. Drift and selection further act to shift allele frequencies following colonization, with a commonly observed selection pressure being reduced capacity for dispersal in island populations. Assemblage-level tests of the importance of these generalities are rare but can allow insights into the strength of linkages between genetic differentiation, species interactions, and community assembly in island ecosystems. Here, we use genomic datasets from nine ant species for which we obtained paired, island-mainland samples, to test the following predictions. (i) Island populations support reduced levels of genetic diversity compared to conspecific mainland populations. (ii) Island populations exhibit greater population genetic structure, which would be consistent with the evolution of reduced dispersal capacity. For each species, we collected samples from ten locations along ~30 km transects on Santa Cruz Island, California and the adjacent mainland (Lompoc Valley). We used targeted enrichment of ultraconserved elements (UCEs) to obtain sequences of orthologous nuclear loci, and extracted SNP data from phased UCE reads. We also obtained several key morphometric measurements for one gyne of each species to test for relationships between gyne body size and estimates population genetic structure. The first prediction was mostly not supported: across the full complement of species, estimates of genetic diversity (e.g., heterozygosity, allelic richness, Tajima's D, Watterson's θ) did not significantly differ between mainland and island populations. In the

comparison of Watterson's θ, however, all but one species exhibited a pattern of smaller values of θ in island populations. The second prediction was also not met. Mainland populations exhibited significantly *greater* pairwise genetic distances between samples. Furthermore, we did not find a significant relationship between gyne body size and population genetic structure. STRUCTURE plots and pairwise Fst values revealed that island and mainland populations exhibited substantial interspecific variation in Fst values (0.007 to 0.46). These results illustrate that island populations may not always conform to theoretical expectations. The age (7.5 my) and size (249 km^2) of Santa Cruz Island could both contribute to current levels of genetic diversity, whereas strong prevailing winds on the island could play a role in the dispersal of reproductives and reduce population structure as a consequence.

INTRODUCTION

Islands populations can offer rare insights into the relative strength of different evolutionary forces. Given the discrete nature of islands and their restricted area, island populations typically support reduced levels of genetic diversity compared to mainland populations (Frankham 1997). Founder effects and population bottlenecks, for example, reduce effective population size (England et al. 2003, Nei and Chakraborty 1975) and increase the importance of genetic drift (Motro and Thompson 1982, Vucetich and Waite 1999). Island area and isolation further influence the genetic structure and diversity of insular populations (Frankham 1997, Jaenike 1973, Losos and Ricklefs 2009) and affect the frequency of gene flow from mainland populations or other islands (Karron 1987). Although most comparisons of mainland and island populations focus on one or a few species (Zheng et al. 2018, Francisco et al. 2016, Dodd and Helenurm 2002, Wauters et al. 2018), the evolution of island populations can be strongly influenced by the presence of other species. Assemblage-level tests of how island populations differ from mainland populations can thus shed light on how genetic differentiation is linked to community assembly and species interactions in island ecosystems (Gillespie et al. 2012, Gillespie et al. 2018).

In addition to reduced genetic diversity, island populations experience selection pressures that differ from those on the mainland. Reductions in dispersal ability, for example, occur in a wide range of insular organisms including plants, birds, and arthropods (Medeiros et al. 2011, Kavanagh and Burns 2014, Wright et al. 2016, Gillespie et al. 2018, Hume et al. 2019, Waters 2020). Although the ability to disperse provides numerous ecological advantages (Bonte et al. 2014), dispersal is energy intensive and risky (Bonte 2012), and terrestrial species that colonize islands can trade-off dispersal ability for enhanced reproductive success (Braendle et al 2006, Hughes and Dorn 2006). Additionally, studies on passively dispersing organisms suggest that reduced capacities for dispersal can decrease the chances of aerially dispersing propagules being transported off-island or beyond the bounds of narrowly distributed habitat types (Carlquist 1966, Carlquist 1974, Carlquist 1980, Roff 1986). While many studies have noted reductions in dispersal abilities within island populations by examining entirely flightless species (Wagner et al. 1992, Medeiros and Gillespie 2011, Wright et al. 2016), fewer studies have examined reduced capacity for dispersal by comparing population genetic structure conspecific island and mainland populations (Waters 2020). Such comparative studies are important because reduced dispersal capacity can also impact the genetic substructuring of species (Gaston 2003). Moreover, disparities in dispersal ability may also affect community assembly by influencing the frequency of propagules arriving at a particular location (Andersen et al. 2008, Livingston and Jackson 2014, King and Tschinkel 2016).

Contemporary studies of population differentiation and selection largely rely on the analysis of molecular sequence data (Hahn 2019), and advances in the sequencing of large, orthologous sets of genetic loci has revolutionized among-lineage comparisons of divergence and genetic diversity (Winker et al. 2018, Stiller et al. 2020). The use of high-throughput sequencing data, when applied to assemblage level comparisons of populations genetic diversity and structure, can provide powerful insights into the mechanisms driving population differentiation. Sequence data from ultraconserved elements, for example, has recently clarified that upland forest bird species exhibit higher genetic diversity and population differentiation in comparison to closely related taxa that occur in floodplains (Harvey et al. 2017). However, these tools are currently underutilized in testing evolutionary processes in insular populations.

A targeted bait set of ultraconserved elements (UCEs) has also been developed for ants (Branstetter et al. 2017), which has enabled robust analyses of the phylogenetic relationships across the ant tree of life (Blaimer et al. 2018, Branstetter et al. 2019, Williams et al. 2020). Ants helped to inspire important theories of island biogeography (Wilson 1961, MacArthur and Wilson 1967, Cole 1983, Vepsäläinen and Pisarski 1982) and have also been the target of contemporary tests of evolution in insular systems (Economo and Sarnat 2012, Matos-Maraví et al. 2018, Sarnat and Moreau 2011). Most ant species produce aerially dispersing, winged reproductives (Hölldobler and Wilson 1990, Ward 2006, Helms 2018), and winged gynes (i.e., queens prior to mating) vary in size and colony founding strategy (Helms 2018). Moreover, species differ with respect to the timing of mating flights and colony founding (Hölldobler and Wilson 1990). Given that winged gynes are responsible both for dispersing from their natal colony and founding a new colony, an evolutionary trade-off exists between dispersal ability, and carrying nutritional loads for colony foundation, at least in species with independent colony founding (Helms and Kaspari 2014, Helms and Kaspari 2015, Helms 2018). Increasing body size allows gynes to fly farther (Helms 2018), but decreases their ability to take advantage of rising air currents and to fly at higher altitudes (Dudley 2000, Dillon et al. 2006). Given these trade-offs, the morphology of ant gynes likely influences dispersal ability and in turn population genetic structure (Pamilo et al. 1992, Chapuisat et al. 1997, Sundstrom et al. 2005), and community assembly (Andersen et al. 2008, Livingston and Jackson 2014, King and Tschinkel 2016).

Here, we use high-throughput sequence data from ultraconserved elements to conduct a multi-species comparison of ant species from Santa Cruz Island, California and an area of comparable size on the adjacent mainland to test for differences in genetic diversity and population genetic structure in mainland and island ant populations. We used genomic datasets from nine ant species to test the following predictions: (i) island populations support reduced levels of genetic diversity compared to conspecific mainland populations, and (ii) island populations exhibit greater population genetic structure, which would be consistent with the evolution of reduced dispersal capacity. In relation to the second prediction, we also test if population genetic structure can be predicted by species-level variation in the morphology of gynes. Our study provides novel insights to genetic differentiation on islands by testing these predictions across an ant assemblage using genomic datasets.

METHODS

Sampling and study area

We conducted sampling for this study on Santa Cruz Island, California and a comparably sized area in the Lompoc Valley, California. Santa Cruz Island (249 km^2 in area) lies 30 km from the mainland and has never been connected to this landmass. As recently as the last glacial maximum, however, Santa Cruz Island and the remaining northern Channel Islands formed a single land mass (Schoenherr et al. 2003). The Lompoc Valley, approximately 100 km northwest of Santa Cruz Island, encompasses the lower portions of the Santa Ynez River watershed (Fig.1). These sampling areas resemble each other in terms of their topography, climate, vegetation, and also broadly overlap in the species of native ants that are present. In each of these two areas, we established ten sampling locations along an E-W transect (Fig. 1). Sampling locations were separated from one another by approximately 3 km (Fig. 1). At each sampling location on both transects, we collected workers of nine ant species: *Dorymyrmex insanus*, *Pheidole hyatti*, *Formica moki*, *Monomorium ergatogyna*, *Crematogaster marioni*, *Prenolepis imparis*, *Camponotus hyatti*, *Solenopsis molesta*, and *Tapinoma sessile*. These ants commonly occur together in scrub ecosystems in this region (Naughton et al. 2020). Samples were collected directly into 95% EtOH. Sampling took place over multiple collecting trips to each area between March and August 2019; and the exact sampling localities for each sample are listed in Table 3-S1. Although we aimed to collect ten samples of each species across collection localities, one species (*Crematogaster marioni*), proved to be rare in the Lompoc Valley and we only found this species at six sampling locations on the mainland.

UCE library prep and bioinformatics

To generate genetic data for the comparison of genetic diversity and structure in mainland and island populations, we conducted high throughput sequencing of UCEs. We used Qiagen DNeasy Blood & Tissue kits (Valencia, CA.) to extract total genomic DNA from ant samples (after removing gasters from all workers). We made the following modifications to the Qiagen kit protocol to optimize small amounts of starting tissue: samples were first ground on a bead mill for 1 min at 3200 rpm, then we added 50µg RNase A and 10µL DTT to the lysis step. We eluted samples in 300µL RNase/DNase free water, then concentrated to samples 100µL using an Eppendorf Vacufuge. Following extraction, we quantified samples using an Invitrogen™ Qubit™ 1X dsDNA HS kit, then sheared samples using a Bioruptor sonicator (Diagenode) for 1 min total shearing time (15 sec shearing time, 90 sec rest for four repetitions). We used Sera-Mag™ Magnetic SpeedBeads in PEG mixture to clean sheared DNA samples to retrieve desired fragment sizes (400 – 1000 bp in length). We used KAPA DNA Hyperprep kits to conduct end repair and A-tailing on each sample, then amplified each sample with Integrated DNA Technologies xGen^{TM} UDI Primer Pairs and xGen Stubby Adapters, for 12 cycles using KAPA HiFi Hotstart Ready Mix. Following index PCR, we quantified libraries and visualized each library on a gel (1.5% Agarose, 80 V for 60 min) to ensure target fragment sizes (400 – 900 bp) had been acquired.

To perform targeted enrichment on pooled libraries, we used a UCE bait set of custom-designed probes targeting 2,590 UCE loci in ants (Branstetter 2017). We followed library enrichment procedures for Arbor Biosciences MyBaits kit (Arbor Biosciences, Inc) to set up bait hybridization, and hybridized RNA baits to libraries at 65C for 24 h. We amplified enriched libraries using universal Illumina primers and 18 PCR cycles, and purified PCR product using a 1.2X SPRI bead clean. To verify enrichment of our libraries, we conducted a qPCR assay (Faircloth et al. 2013a) on five pairs per each lane of sequencing of unenriched and post-enriched libraries using DyNAmo™ Flash SYBR®Green qPCR kit (Thermo Fisher Scientific) to amplify three UCEs in each library (UCE82, UCE591, UCE1481). After qPCR verification, we sent enriched samples to the Vincent J. Coates Genomic Sequencing lab at UC Berkeley, where peak fragment size of each pool was checked on a Bioanalyzer prior to pooling at equimolar concentrations into a single lane and sequenced on an Illumina NovaSeq platform. Our samples were sequenced in two lanes of sequencing, under the same protocols.

After sequence data were demultiplexed and converted to FASTQ format by the Vincent J. Coates Genomics Sequencing laboratory, we processed sequence data to obtain SNP data and UCE alignments for each species. We used ILLUMIPROCESSOR (Faircloth 2013b) to clean and trim raw FASTQ reads and remove low quality reads. The read count and length measurements of trimmed reads for each sample are listed in Table 3-S2. To maximize the number of UCE regions recovered and the length of the flanking regions, we used SPAdes (Prjibelski 2020) to assemble contigs with a range of *k*-mers of 21, 33, and 55, then selected the longest contig for overlapping UCEs. We matched assembled contigs to UCE loci and generated a sqlite database of all UCE reads for each sample using the PHYLUCE program phyluce_align_match_contigs_to_probes, then aligned all loci in a wrapper script (phyluce_align_seqcap_align) around MAFFT v.7.130b (Katoh et al. 2013). We retained aligned loci that contained 75% or more of our samples for allele phasing.

To obtain data for measuring genetic diversity and population genetic structure, and the construction STRUCTURE plots, we phased our UCE sequences and extracted one SNP per UCE locus from phased reads. Allele phasing effectively identifies variable positions within a target locus of an individual; these positions are typically lost during contig assembly, as most assembly algorithms produce only the more numerous variant while discarding alternative variants (Andermann 2019). For each sample, we mapped raw fastq reads against reference contigs and marked read duplicates with SAMtools (Li et al. 2011), added read groups with Picard (http://broadinstitute.github.io/picard/), and constructed a BAM file using bwa-mem (Li et al. 2009). We used the Phyluce script phyluce_snp_phase_uces to analyze and sort reads within the BAM file for each sample into reads for each allele and create fasta files for UCE reads. We aligned phased fasta files then called SNPs using the Phyluce script phyluce_snp_screen_phased_alignments. We used a custom python script (https://github.com/dportik) to extract one SNP per locus at random and concatenate SNPs into a datamatrix for use in the program STRUCTURE.

We constructed alignments of UCE loci to estimate nucleotide diversity, Tajima's D, and Watterson's θ, which rely on calculating the number of segregating sites in a gene sequence. We used the sqlite database generated from matching assembled contigs to UCE probes to generate separate monolithic fasta files for all samples of each species, then we aligned all loci using a wrapper script (phyluce_align_seqcap_align) around MAFFT v.7.130b (Katoh et al. 2013). We left out the incomplete-matrix option while constructing alignments, resulting in our alignments containing only UCE loci that were sequenced across all samples in a species dataset. The number of resulting UCE loci for each species dataset is noted in Table 3-S4.

Population genetic analyses

We used STRUCTURE 2.3.4 (Pritchard et al. 2000) to analyze SNP data under the admixture model and to estimate the degree of gene flow between mainland and island populations for each species dataset. We assumed different numbers of genetic demes from

K = 2 to K = 6 for 100,000 generations with a burn in of 50,000 and three replicates at each value of K. We used STRUCTURE-Harvester (Earl 2012) to determine the most likely number of genetic demes based on the Evanno method (Evanno 2005). We used PGDSpider v.2.1.1.5 (Lischer and Excoffier 2012) to convert STRUCTURE files to input files for Arlequin 3.5.2.2 (Excoffier et al. 2010). In Arlequin, we calculated pairwise Fst values between mainland and island populations, and observed and expected heterozygosity (Ho, He) for each population. We used our SNP data matrices to estimate rarefied allelic richness and average pairwise genetic distance (Nei's standard genetic distance, Nei et al. 1987) for island and mainland populations using the packages Adegenet 2.1.3 (Jombart 2008) and hierfstat (Goudet 2005) implemented in R 3.6.2 (R Core Team 2019). For rarefied allelic richness, the number of alleles used for rarefaction is equal to half the number of individuals in the dataset. We used the R package PopGenome 2.7.5 (Pfeifer et al. 2014) to read in and concatenate UCE alignments and to estimate genetic diversity statistics (Tajima's D, Watterson's θ, nucleotide diversity). We determined measures of nucleotide diversity in PopGenome 2.7.5 by determining the total number of polymorphic sites in the alignment, and dividing by the total number of sites. To compare values of genetic diversity and differentiation between mainland and island populations, we checked that the differences between mainland and island populations were normally distributed using a Shapiro-Wilks test in R, then performed paired t-tests between island and mainland populations.

Analyses of gyne morphology

To determine if population structure can be predicted from gyne morphology (i.e., based on traits linked to flight ability) we tested for relationships between average pairwise genetic distance and specific morphological traits (Weber's length, head width, wing length, wing length/Weber's length). Weber's length (posterior-ventral point of thorax in lateral view, to anterior-dorsal point of thorax in lateral view), and head width are standard measures of ant body size (Brown 1953, Helms 2018), whereas wing length is considered to be important for dispersal ability (Greenleaf 2007). To obtain morphological measurements for winged gynes, we used high-resolution, photomontage images from Antweb (www.antweb.org) and AntWiki (www.antwiki.org). We obtained morphometric data from one gyne of all nine focal ant species. For one species (*Monomorium ergatogyna*) we were unable to find a winged gyne specimen image, so we estimated wing length by calculating the proportion of wing length to Weber's length of a closely related species (*Monomorium minimum*) and used this proportion to estimate *M. ergatogyna* wing length based on the Weber's length of *M. ergatogyna*. Morphometric measurements for gynes of each species are listed in Table 3-S3. We then conducted linear regressions for morphological traits and measures of genetic distance using the stats package in R (R core team 2019). Although the morphology of male ants, which are also winged, likely also affects patterns of gene flow and population genetic structure, we were unable to find images of males for most species.

RESULTS

Contrary to our first prediction, none of the assemblage-level comparisons of genetic diversity differed significantly between island and mainland populations (Table 3-1). Observed heterozygosity, for example, was higher in island populations compared to mainland populations, for seven of the nine ant species considered. Although other measures of genetic diversity did not differ between island and mainland populations (Table 1), Watterson's θ exhibited a pattern in which island populations of all species (except for *C. marioni*) had lower values compared to mainland populations (Fig. 3-2). If *C. marioni* is excluded from the analysis, island populations exhibit significantly higher estimates of Watterson's θ compared to mainland populations. The paired t-test result of Watterson's θ if *C. marioni* is excluded is as follows: $p = 0.0038$, t = 4.2469.

Our second prediction was also refuted. Mainland populations exhibited *higher* values of pairwise genetic distance compared to island populations (Table 3-2, Fig. 3-4). Measures of average pairwise genetic distance ranged from 0.02327 (*T. sessile*) to 0.13726 (*C. marioni*) in island populations, and from 0.07444 (*D. insanus*) to 0.18213 (*S. molesta*) in mainland populations (Table 3-2). Estimates of average pairwise genetic distance were higher within mainland populations across all species except for *C. marioni*, which exhibited higher genetic distance within the island population. STRUCTURE plots further illustrated only weak population structure for some island populations (e.g. *P. hyatti* and *C. hyatti*) (Fig. 3-4). The STRUCTURE plot for *S. molesta* (Fig. 3-4) contains a sample that formed a separate genetic deme within the mainland population; the species identity of the sample was checked carefully after this result, and this sample does not form a separate genetic deme from the remaining *S. molesta* in mainland and island populations when the number of assumed populations (K) is reduced to 2 (Fig. 3-S1).

STRUCTURE plots and Fst values also revealed interspecific variation with respect to the degree of genetic differentiation between mainland and island populations. Mainland and island samples of *C. hyatti* and *F. moki*, for example, were separated into distinct genetic demes, whereas mainland and island populations of *M. ergatogyna* (Fig. 2D) and *P. imparis* appeared panmictic (Fig. 3-4). STRUCTURE plots were largely corroborated by pairwise Fst values between mainland and island populations for each species (Fig. 3-4). Pairwise Fst was lowest between mainland and island samples of *M. ergatogyna* (0.00727) and highest between samples of *C. hyatti* (0.46004). Furthermore, linear regressions did not reveal a significant relationship between morphometric measurements and average pairwise genetic distance (Table 3-3).

DISCUSSION

Through the use of phylogenomic data from island and mainland populations of nine different ant species, our study provides a unique assemblage-level test of how island and mainland populations differ from one another. Our results were somewhat unexpected. First, we observed no differences in genetic diversity between mainland and island populations in comparisons that used heterozygosity, allelic richness, Tajima's D, and nucleotide diversity as response variables. For comparisons involving Watterson's θ, an estimate that scales with effective population size, all but one species (*C. marioni*) in our analysis had lower values in island populations compared to mainland populations. These findings suggest that island size and age are important factors influencing levels of genetic diversity in island populations. Second, mainland populations supported higher levels of population genetic structure compared to island populations. This latter finding in turn suggests lower levels of intra-population dispersal in mainland populations compared to that in island populations. Lastly, although we observed no strong relationships between gyne morphology and population-level differentiation, there was striking species-level variation both in terms of population-level differentiation and the distinctness of island and mainland populations.

Despite the fact that island populations are often considered to support reduced levels of genetic diversity (Frankham et al. 1997, Whittaker 2007), exceptions to this pattern exist, especially for islands that are within the dispersal capabilities of the organisms in question (Fernández-Mazuecos, and Vargas 2011, García-Verdugo, Kaueffer et al. 2007, McLaughlin et al. 2014, Francisco et al. 2016). Across the full set of species in our assemblage, we found that mainland and island populations did not significantly differ with respect to measures of genetic diversity. A number of processes may be contributing to the maintenance of genetic diversity in Santa Cruz Island populations. Santa Cruz Island is relatively large and within 30 km of the mainland, and thus may receive moderate levels of gene flow and support levels of genetic diversity that are higher than if the island was smaller or more isolated (e.g., Losos and Ricklefs 2009). Gene flow from the mainland is evident in the low Fst values between mainland and island samples for at least some of the species in our study (e.g. *M. ergatogyna* and *P. imparis*). Furthermore, Santa Cruz Island is a relatively old island (~7.5 my), and could thus harbor ancestral genetic diversity (Aleixandre et al. 2013). Interestingly, *C. marioni* was the only species for which the estimate of Watterson's θ was higher in the island population compared to the mainland population. Since Watterson's θ scales with effective population size (Klein et al. 1999), this finding suggests that the mainland population size of *C. marioni* may be constrained in comparison to the island population. On the mainland, *C. marioni* was rare and restricted to a particular habitat type, whereas this species is common and widespread on Santa Cruz Island (as well as on the other islands on which it occurs). This finding may suggest that Santa Cruz Island supports a higher effective population size of *C. marioni* compared to the mainland population, perhaps resulting from ecological release from predators in *C. marioni* island populations.

Our finding that mainland populations, relative to island populations, supported higher levels of pairwise genetic distance was unexpected given that evolution for reduced dispersal ability is commonly observed in island organisms, especially those that disperse aerially (Wauters et al. 2020). This finding, and the lack of strong relationships between morphology and pairwise genetic distance (Table 3), could be explained by higher prevailing wind speeds on Santa Cruz Island compared to the mainland. The impacts of wind on dispersing insects are incompletely understood, but even moderate increases in wind speed increase dispersal distances in *Drosophila* (Leitch et al. 2020). Wind assisted dispersal could potentially influence dispersal distance for small gynes in particular, given that smaller queens are more likely to fly at higher altitudes (Dudley 2000, Dillon et al. 2006), and it is notable that the second smallest gyne (*M. ergatogyna*) also exhibited the lowest Fst value between mainland and island populations, while the species with the largest gyne (*C. hyatti*) exhibited the highest Fst value. The absence of a significant pattern between species body size and population differentiation suggests that alternative morphological traits of gynes may influence intra-population dispersal capacity more than body size. Abdominal mass, for example, has been found to correlate with nutritional loading of crucial stores for early stages of colony founding, but heavier abdominal masses can also increase drag during flights (Helms and Kaspari 2014, 2015). Wing-loading (wing surface-area to thoracic volume) has also been found to significantly influence dispersal capacity in ants and bees (Greenleaf 2007, Helms and Godfrey 2016, Riley et al. 2016). Furthermore, variation in aerial mating behaviors may further influence dispersal ability, as species that form aerial mating swarms might be more likely to be take advantage of wind-assisted dispersal than species that form leks at ground level (Hölldobler and Wilson 1990).

Islands have proven to be invaluable natural laboratories to test how evolutionary processes affect genetic diversity and capacity for dispersal (MacArthur and Wilson 1967, England et al. 2003, Frankham 1997, Jaenike 1973, Losos and Ricklefs 2009, Gillespie et al.

2018, Hume et al. 2019). Testing for population differentiation across an assemblage of species is a useful framework for detecting broad evolutionary trends, such as the role of genetic differentiation in community assembly (Gillespie et al. 2018), or the effects of habitat association on genetic diversity and differentiation across species (Harvey et al. 2017). Using an assemblage-level comparison of ants based on genomic data, our study provides novel insights to genetic diversity and differentiation on islands and highlights the importance of further investigation into the mechanisms by which islands can retain genetic diversity and intra-population connectivity.

ACKNOWLEDGEMENTS

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Chapter 3, in part, is currently being prepared for submission for publication of the material. Naughton, I., Tsutsui, N.D., Ward, P.S., and Holway, D.A. The dissertation author was the primary investigator and author of this material.

Table 3-1. Genetic diversity measurements for mainland (LPC = Lompoc Valley) and island (SCR = Santa Cruz Island) populations of nine ant species. Ho, He, GD, and Na measurements based on SNP data (one SNP per UCE locus), whereas π, D, and θ_w are based on aligned UCE reads for each species. Mainland-island species pairs were compared for significant differences based on paired *t*-tests.

	Observed Heterozygosity (Ho)		Expected Heterozygosity (He)		Allelic Richness (Na)		Nucleotide diversity (π)		Tajima's D (D)		Watterson's θ (θw)	
Species	**LPC**	**SCR**	**LPC**	**SCR**	**LPC**	**SCR**	**LPC**	**SCR**	**LPC**	**SCR**	**LPC**	**SCR**
Monomorium ergatogyna	0.45129	0.49216	0.39955	0.40739	1.7146	1.6913	0.00196	0.00184	0.50379	1.24347	2.15166	1.68962
Prenolepis imparis	0.13983	0.24012	0.16434	0.25838	1.4683	1.2281	0.00061	0.00058	-1.01522	-0.64654	0.80969	0.68940
Crematogaster marioni	0.18733	0.10673	0.34133	0.22280	1.1489	1.3239	0.00110	0.00097	-1.33655	-1.92474	1.07977	2.15623
Solenopsis molesta	0.12514	0.22287	0.28949	0.35003	1.4098	1.1604	0.00109	0.00082	-1.09031	-0.65571	1.22346	0.75749
Pheidole hyatti	0.19164	0.19564	0.28642	0.25510	1.3546	1.4096	0.00073	0.00109	-1.26753	-1.23521	2.15712	1.48473
Formica moki	0.17086	0.16526	0.23590	0.20820	1.1351	1.3813	0.00096	0.00076	-0.86449	-0.87161	1.11987	0.92028
Dorymyrmex insanus	0.05536	0.08207	0.12758	0.19310	1.4051	1.1795	0.00054	0.00043	-2.20074	-1.77304	0.93184	0.49551
Tapinoma sessile	0.03531	0.07889	0.24623	0.19509	1.0940	1.0393	0.00120	0.00042	-1.19624	-1.40439	1.13554	0.43989
Camponotus hyatti	0.14792	0.16355	0.22199	0.17788	1.3048	1.0544	0.00161	0.00053	-0.72091	-1.07744	1.87414	0.58768
Paired t-test results	p	0.1792	p	0.8316	p	0.3540	p	0.26200	p	0.3875	p	0.1242
	t	1.477	t	0.2197	t	0.9838	t	1.2122	t	0.9193	t	1.7174

Table 3-2. Estimates of average pairwise genetic distance for mainland (LPC = Lompoc Valley) and island (SCR = Santa Cruz Island) populations of nine ant species. Estimates were calculated using Nei's genetic distance (Nei 1987) and based on SNP data (one SNP per UCE locus).

Average Pairwise Genetic Distance (GD)		
Species	**LPC**	**SCR**
Monomorium ergatogyna	0.15333	0.12800
Prenolepis imparis	0.08689	0.06956
Crematogaster marioni	0.11670	0.13726
Solenopsis molesta	0.18213	0.12640
Pheidole hyatti	0.14328	0.11716
Formica moki	0.09416	0.06794
Dorymyrmex insanus	0.07444	0.05909
Tapinoma sessile	0.12190	0.02327
Camponotus hyatti	0.11592	0.03088
Paired t-test results	p	0.0181
	t	3.3402

Table 3-3. Linear regressions testing the relationships between gyne morphology and population genetic structure. GD = measurements of average pairwise genetic distance within a population (average of island and mainland GD), HW = gyne head width, WL = Weber's Length, WI = wing length, WI / WL = wing length divided by Weber's length.

Independent variable	**Response variable**	**R^2**	**df**	**F**	**p**
HW	GD	-0.0810	1,7	0.400	0.547
WL	GD	-0.0380	1,7	0.708	0.428
WI	GD	-0.0646	1,7	0.515	0.496
WI / WL	GD	-0.0490	1,7	0.621	0.457

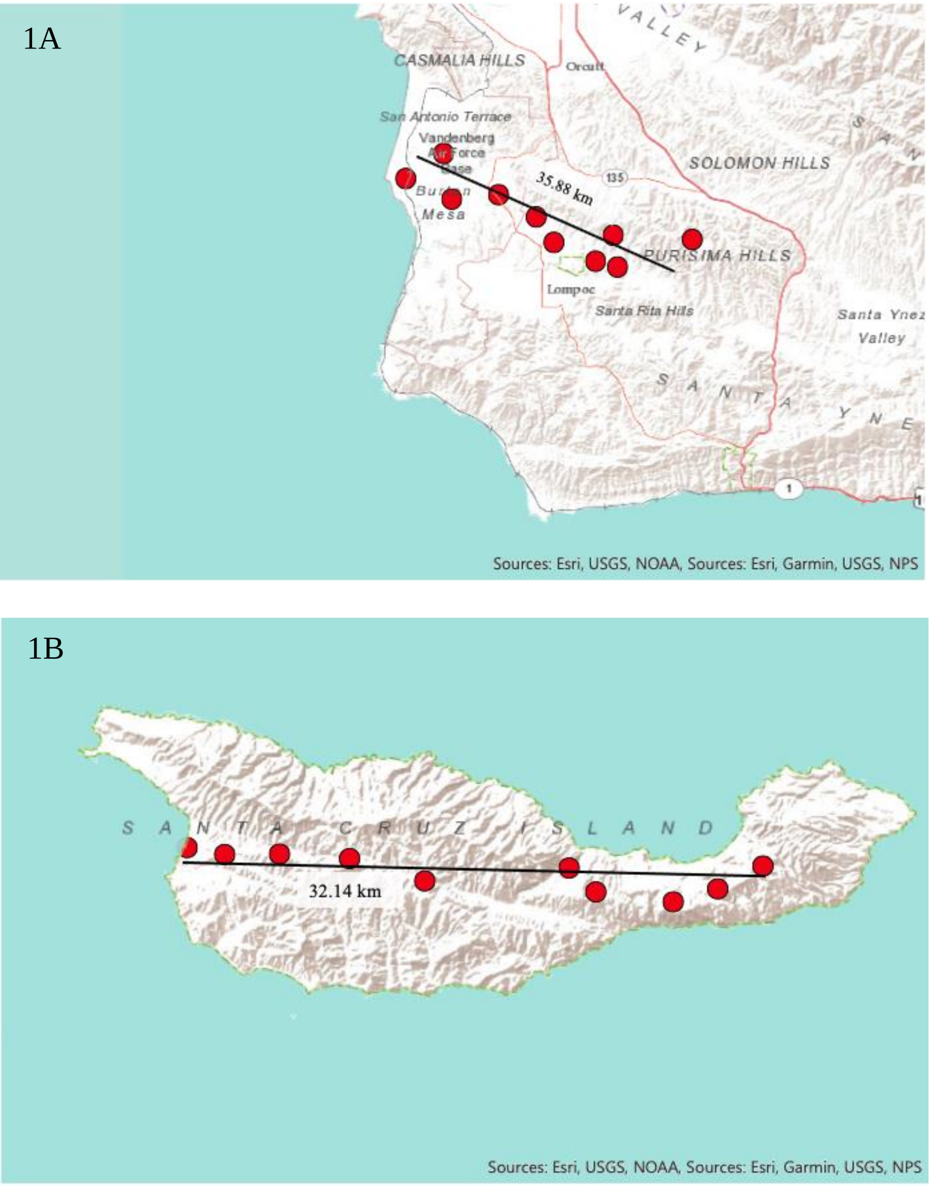


Figure 3-1. Map of mainland (A - Lompoc Valley) and island (B – Santa Cruz Island) sampling areas. Collection locations along each transect are indicated by red circles.

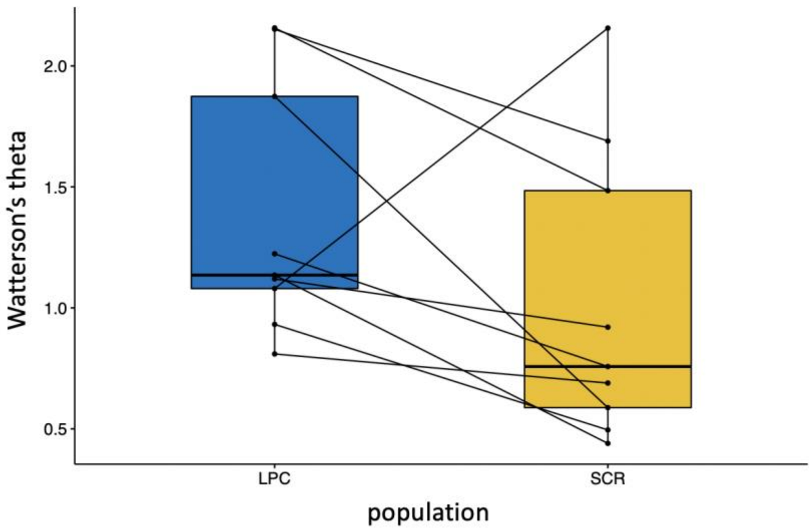


Figure 3-2. Estimates of Watterson's θ for mainland (LPC = Lompoc) and island (SCR = Santa Cruz Island) populations. Lines connect species pairs. *Crematogaster marioni* represents the only species for which estimates of Watterson's θ were higher in the Mainland than in the island population.

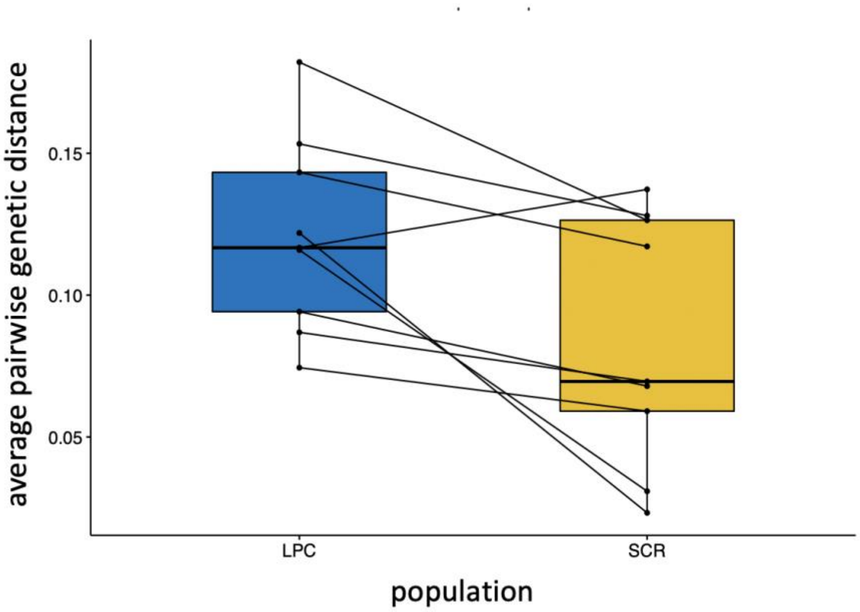
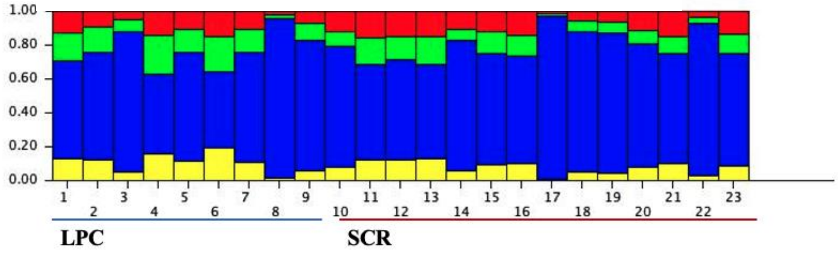


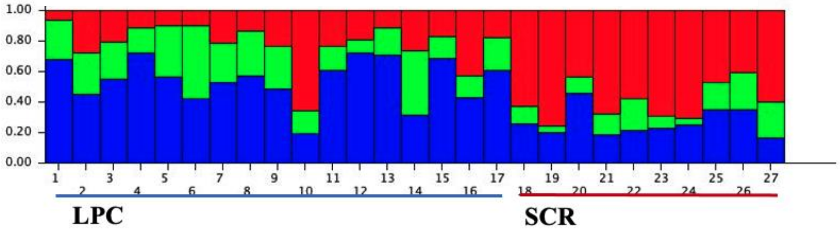
Figure 3-3. Average pairwise genetic distance for mainland (LPC = Lompoc Valley) and island (SCR = Santa Cruz Island) populations of nine ant species. Lines connect species pairs. *Crematogaster marioni* represents the only species for which estimates of genetic distance were higher in the island population compared to the mainland population.

Figure 3-4. STRUCTURE plots based on SNP data for mainland (LPC = Lompoc Valley) and island (SCR = Santa Cruz Island) populations of nine ant species: **(A)** *Monomorium ergatogyna* (K = 4, n = 839 SNPS, **(B)** *Prenolepis imparis* (K=3, n = 1908 SNPs), **(C)** *Crematogaster marioni*, (K= n = 1273 SNPs), **(D)** *Solenopsis molesta* (K = 4, n = 1975 SNPs), **(E)** *Pheidole hyatti* (K = 3, n = 1669 SNPs), **(F)** *Formica moki* (K = 3, n = 1062 SNPs, **(G)** *Dorymyrmex insanus* (K = 3, n = 1386 SNPs), **(H)** *Tapinoma sessile* (K = 3 n = 1014 SNPs), **(I)** *Camponotus hyatti* (K = 3, n = 2013 SNPs). The value of K selected was based on the Evanno method (Evanno et al. 2005).

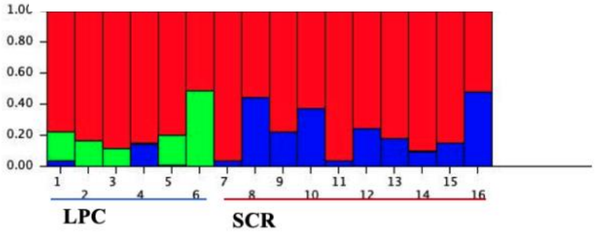
4A. *Monomorium ergatogyna*, Fst = 0.00727



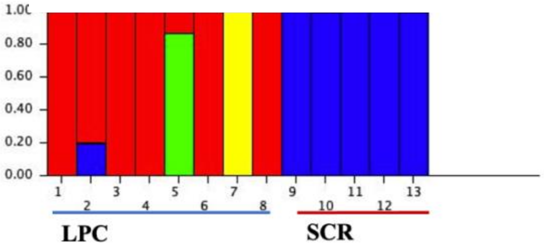
4B. *Prenolepis imparis*, Fst = 0.07561



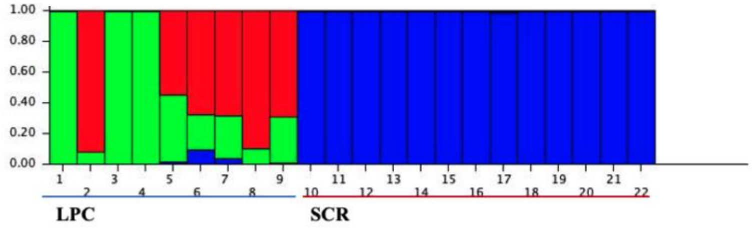
4C. *Crematogaster marioni*, Fst = 0.12209



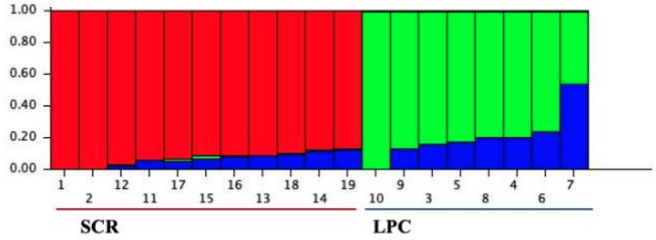
4D. *Solenopsis molesta*, Fst = 0.12742



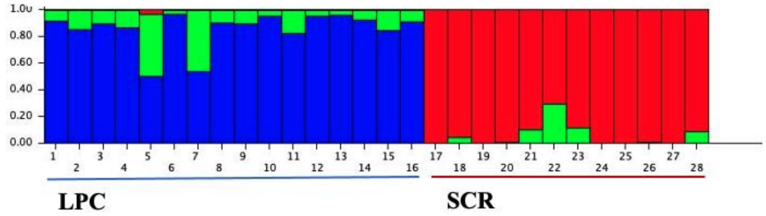
4E. *Pheidole hyatti*, Fst = 0.15956



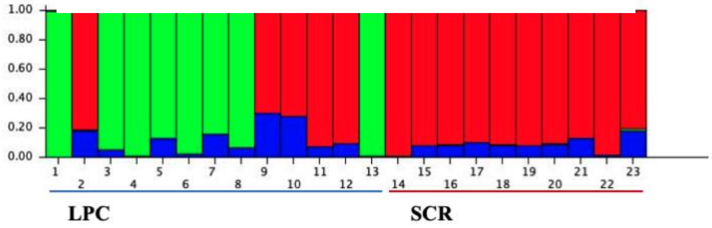
4F. *Formica moki*, Fst = 0.21463



4G. *Dorymyrmex insanus*, Fst = 0.23554



4H. *Tapinoma sessile*, Fst = 0.34546



4I. *Camponotus hyatti*, Fst = 0.46004

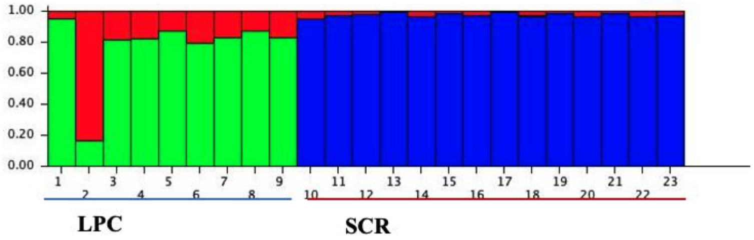


Figure 3-4. STRUCTURE plots based on SNP data for mainland (LPC = Lompoc Valley) and island (SCR = Santa Cruz Island) populations of nine ant specie, *continued*.

Table 3-S1. Sample collection information.

ID	**Species**	**Population**	**Lat**	**Long**	**Collector**	**Date**
INM625	*Monomorium ergatogyna*	Lompoc Valley	34.73336	-120.59122	Ida Naughton	3.vii.19
INM626	*Monomorium ergatogyna*	Lompoc Valley	34.71293	-120.47790	Ida Naughton	4.vii.19
INM627	*Monomorium ergatogyna*	Lompoc Valley	34.73700	-120.56075	Ida Naughton	3.vii.19
INM628	*Monomorium ergatogyna*	Lompoc Valley	34.74174	-120.50670	Ida Naughton	3.vii.19
INM637	*Monomorium ergatogyna*	Lompoc Valley	34.61354	-120.55660	Ida Naughton	24.iii.19
INM636	*Monomorium ergatogyna*	Lompoc Valley	34.75539	-120.62060	Ida Naughton	24.iii.19
INM633	*Monomorium ergatogyna*	Lompoc Valley	34.68441	-120.42220	Ida Naughton	16.v.19
INM632	*Monomorium ergatogyna*	Lompoc Valley	34.72066	-120.46420	Ida Naughton	19.iv.19
INM631	*Monomorium ergatogyna*	Lompoc Valley	34.78347	-120.53067	Ida Naughton	21.iv.19
INZ869	*Monomorium ergatogyna*	Santa Cruz Island	34.02359	-119.87350	Ida Naughton	12.iv.19
INZ866	*Monomorium ergatogyna*	Santa Cruz Island	34.00626	-119.75820	Ida Naughton	12.iv.19
INZ864	*Monomorium ergatogyna*	Santa Cruz Island	34.01244	-119.59597	Ida Naughton	15.iv.19
INZ863	*Monomorium ergatogyna*	Santa Cruz Island	34.01158	-119.69050	Ida Naughton	15.iv.19
INZ862	*Monomorium ergatogyna*	Santa Cruz Island	33.99913	-119.76180	Ida Naughton	25.viii.16
INZ861	*Monomorium ergatogyna*	Santa Cruz Island	33.99912	-119.82179	Ida Naughton	25.viii.16
INZ860	*Monomorium ergatogyna*	Santa Cruz Island	34.04268	-119.93010	Ida Naughton	7.viii.16
INZ855	*Monomorium ergatogyna*	Santa Cruz Island	34.00396	-119.86715	Ida Naughton	5.viii.16
INZ856	*Monomorium ergatogyna*	Santa Cruz Island	34.00396	-119.86160	Ida Naughton	5.viii.16
INZ857	*Monomorium ergatogyna*	Santa Cruz Island	34.04681	-119.56738	Ida Naughton	8.vii.16
INZ873	*Monomorium ergatogyna*	Santa Cruz Island	34.00307	-119.61801	Ida Naughton	27.vii.19
INZ858	*Monomorium ergatogyna*	Santa Cruz Island	33.99973	-119.82131	Ida Naughton	4.viii.16
INZ868	*Monomorium ergatogyna*	Santa Cruz Island	34.01126	-119.81517	Ida Naughton	12.iv.19
INZ859	*Monomorium ergatogyna*	Santa Cruz Island	34.04657	-119.88078	Ida Naughton	5.viii.16
INM705	*Prenolepis imparis*	Lompoc Valley	34.63170	-120.57583	Ida Naughton	2.vi.19
INM707	*Prenolepis imparis*	Lompoc Valley	34.78347	-120.53067	Ida Naughton	21.iv.19
INM708	*Prenolepis imparis*	Lompoc Valley	34.68441	-120.42220	Ida Naughton	20.iv.19
INM709	*Prenolepis imparis*	Lompoc Valley	34.68441	-120.42220	Ida Naughton	20.iv.19
INM710	*Prenolepis imparis*	Lompoc Valley	34.70013	-120.28581	Ida Naughton	20.iv.19
INM711	*Prenolepis imparis*	Lompoc Valley	34.68188	-120.43693	Ida Naughton	19.iv.19
INM712	*Prenolepis imparis*	Lompoc Valley	34.72066	-120.46420	Ida Naughton	19.iv.19
INM713	*Prenolepis imparis*	Lompoc Valley	34.70013	-120.28581	Ida Naughton	25.iii.19
INM714	*Prenolepis imparis*	Lompoc Valley	34.72066	-120.46420	Ida Naughton	18.iii.19
INM715	*Prenolepis imparis*	Lompoc Valley	34.69746	-120.44398	Ida Naughton	18.iii.19
INM716	*Prenolepis imparis*	Lompoc Valley	34.68031	-120.39632	Ida Naughton	18.iii.19
INM717	*Prenolepis imparis*	Lompoc Valley	34.67501	-120.37130	Ida Naughton	18.iii.19
INM718	*Prenolepis imparis*	Lompoc Valley	34.53209	-120.17690	Ida Naughton	18.iii.19
INM720	*Prenolepis imparis*	Lompoc Valley	34.69490	-120.47257	Ida Naughton	19.iii.19
INM722	*Prenolepis imparis*	Lompoc Valley	34.69746	-120.44398	Ida Naughton	18.iii.19
INZ874	*Prenolepis imparis*	Santa Cruz Island	34.01724	-119.85255	Ida Naughton	16.iii.19

INZ875	*Prenolepis imparis*	Santa Cruz Island	33.99913	-119.76180	Ida Naughton	17.iii.19
INZ877	*Prenolepis imparis*	Santa Cruz Island	34.02359	-119.87350	Ida Naughton	17.iii.19
INZ878	*Prenolepis imparis*	Santa Cruz Island	34.00631	-119.76087	Ida Naughton	16.iii.19
INZ879	*Prenolepis imparis*	Santa Cruz Island	34.01158	-119.69050	Ida Naughton	15.iii.19
INZ880	*Prenolepis imparis*	Santa Cruz Island	34.01244	-119.59597	Ida Naughton	15.iii.19
INZ883	*Prenolepis imparis*	Santa Cruz Island	34.00183	-119.67745	Ida Naughton	15.iii.19
INZ885	*Prenolepis imparis*	Santa Cruz Island	34.01244	-119.59597	Ida Naughton	11.iv.19
INZ886	*Prenolepis imparis*	Santa Cruz Island	34.01256	-119.78147	Ida Naughton	12.iv.19
INZ887	*Prenolepis imparis*	Santa Cruz Island	34.02359	-119.87350	Ida Naughton	12.iv.19
INM651	*Crematogaster marioni*	Lompoc Valley	34.71088	-120.43612	Ida Naughton	15.v.19
INM650	*Crematogaster marioni*	Lompoc Valley	34.68441	-120.42220	Ida Naughton	16.v.19
INM653	*Crematogaster marioni*	Lompoc Valley	34.70013	-120.28581	Ida Naughton	30.vii.19
INM652	*Crematogaster marioni*	Lompoc Valley	34.67501	-120.37130	Ida Naughton	18.iii.19
INM892	*Crematogaster marioni*	Lompoc Valley	34.77862	-120.57009	Ida Naughton	12.v.20
INM899	*Crematogaster marioni*	Lompoc Valley	34.72066	-120.46420	Ida Naughton	11.v.20
INZ819	*Crematogaster marioni*	Santa Cruz Island	33.99913	-119.76180	Ida Naughton	15.iv.19
INZ816	*Crematogaster marioni*	Santa Cruz Island	34.02452	-119.58340	Ida Naughton	12.v.19
INZ815	*Crematogaster marioni*	Santa Cruz Island	34.00307	-119.61801	Ida Naughton	12.v.19
INZ822	*Crematogaster marioni*	Santa Cruz Island	34.01256	-119.78147	Ida Naughton	12.iv.19
INZ821	*Crematogaster marioni*	Santa Cruz Island	34.01256	-119.78147	Ida Naughton	12.iv.19
INZ820	*Crematogaster marioni*	Santa Cruz Island	34.00626	-119.75820	Ida Naughton	12.iv.19
INZ826	*Crematogaster marioni*	Santa Cruz Island	33.97559	-119.75910	Ida Naughton	26.vii.19
INZ817	*Crematogaster marioni*	Santa Cruz Island	34.00307	-119.61801	Ida Naughton	12.v.19
INZ825	*Crematogaster marioni*	Santa Cruz Island	34.00307	-119.61801	Ida Naughton	23.vi.16
INZ818	*Crematogaster marioni*	Santa Cruz Island	34.05464	-119.78853	Ida Naughton	23.vi.16
INM659	*Solenopsis molesta*	Lompoc Valley	34.68188	-120.43693	Ida Naughton	2.viii.19
INM655	*Solenopsis molesta*	Lompoc Valley	34.61354	-120.55660	Ida Naughton	2.vi.19
INM654	*Solenopsis molesta*	Lompoc Valley	34.73336	-120.59122	Ida Naughton	3.vii.19
INM656	*Solenopsis molesta*	Lompoc Valley	34.78385	-120.53050	Ida Naughton	21.iv.19
INM660	*Solenopsis molesta*	Lompoc Valley	34.74174	-120.50670	Ida Naughton	2.viii.19
INM661	*Solenopsis molesta*	Lompoc Valley	34.70013	-120.28581	Ida Naughton	2.viii.19
INM657	*Solenopsis molesta*	Lompoc Valley	34.72066	-120.46420	Ida Naughton	15.v.19
INM662	*Solenopsis molesta*	Lompoc Valley	34.69746	-120.44398	Ida Naughton	2.viii.19
INM905	*Solenopsis molesta*	Santa Cruz Island	33.99351	-119.63720	Ida Naughton	3.vii.19
INZ738	*Solenopsis molesta*	Santa Cruz Island	34.02452	-119.58340	Ida Naughton	12.v.19
INZ739	*Solenopsis molesta*	Santa Cruz Island	34.00307	-119.61801	Ida Naughton	12.v.19
INZ903	*Solenopsis molesta*	Santa Cruz Island	33.99016	-119.67690	Ida Naughton	15.v.19
INZ904	*Solenopsis molesta*	Santa Cruz Island	33.99422	-119.67520	Ida Naughton	3.vii.19
INM648	*Pheidole hyatti*	Lompoc Valley	34.71088	-120.43612	Ida Naughton	15.v.19
INM643	*Pheidole hyatti*	Lompoc Valley	34.73700	-120.56075	Ida Naughton	3.vii.19
INM640	*Pheidole hyatti*	Lompoc Valley	34.75710	-120.59113	Ida Naughton	3.vi.19

INM646	*Pheidole hyatti*	Lompoc Valley	34.75710	-120.59113	Ida Naughton	20.iv.19
INM647	*Pheidole hyatti*	Lompoc Valley	34.68441	-120.42220	Ida Naughton	16.v.19
INM644	*Pheidole hyatti*	Lompoc Valley	34.68031	-120.39632	Ida Naughton	4.vii.19
INM645	*Pheidole hyatti*	Lompoc Valley	34.61354	-120.55660	Ida Naughton	2.vi.19
INM641	*Pheidole hyatti*	Lompoc Valley	34.68188	-120.43693	Ida Naughton	4.vii.19
INM642	*Pheidole hyatti*	Lompoc Valley	34.73336	-120.59122	Ida Naughton	3.vii.19
INZ746	*Pheidole hyatti*	Santa Cruz Island	34.02452	-119.58340	Ida Naughton	12.v.19
INZ747	*Pheidole hyatti*	Santa Cruz Island	34.01244	-119.59597	Ida Naughton	12.v.19
INZ749	*Pheidole hyatti*	Santa Cruz Island	34.00307	-119.61801	Ida Naughton	12.iv.19
INZ758	*Pheidole hyatti*	Santa Cruz Island	34.00631	-119.76087	Ida Naughton	12.iv.19
INZ748	*Pheidole hyatti*	Santa Cruz Island	34.02452	-119.58340	Ida Naughton	12.v.19
INZ751	*Pheidole hyatti*	Santa Cruz Island	34.04785	-119.55950	Ida Naughton	8.vii.16
INZ750	*Pheidole hyatti*	Santa Cruz Island	34.00810	-119.81142	Ida Naughton	4.viii.16
INZ753	*Pheidole hyatti*	Santa Cruz Island	33.99817	-119.71370	Ida Naughton	25.v.16
INZ752	*Pheidole hyatti*	Santa Cruz Island	34.99973	-119.52131	Ida Naughton	25.viii.16
INZ755	*Pheidole hyatti*	Santa Cruz Island	34.00949	-119.80210	Ida Naughton	30.viii.16
INZ757	*Pheidole hyatti*	Santa Cruz Island	34.00631	-119.76087	Ida Naughton	15.iv.19
INZ759	*Pheidole hyatti*	Santa Cruz Island	34.01256	-119.78147	Ida Naughton	15.iv.19
INZ760	*Pheidole hyatti*	Santa Cruz Island	34.00631	-119.76087	Ida Naughton	12.iv.19
INM894	*Formica moki*	Lompoc Valley	34.68031	-120.39632	Ida Naughton	12.v.20
INM729	*Formica moki*	Lompoc Valley	34.70013	-120.28581	Ida Naughton	20.iv.19
INM728	*Formica moki*	Lompoc Valley	34.74174	-120.50670	Ida Naughton	21.iv.19
INM731	*Formica moki*	Lompoc Valley	34.68441	-120.42220	Ida Naughton	16.v.19
INM737	*Formica moki*	Lompoc Valley	34.63689	-120.18640	Ida Naughton	25.iii.19
INM735	*Formica moki*	Lompoc Valley	34.73854	-120.56538	Ida Naughton	24.iii.19
INM732	*Formica moki*	Lompoc Valley	34.69746	-120.44398	Ida Naughton	15.v.19
INM730	*Formica moki*	Lompoc Valley	34.72066	-120.46420	Ida Naughton	19.iv.19
INZ787	*Formica moki*	Santa Cruz Island	34.00307	-119.61801	Ida Naughton	12.v.19
INZ785	*Formica moki*	Santa Cruz Island	34.00307	-119.61801	Ida Naughton	12.v.19
INZ800	*Formica moki*	Santa Cruz Island	33.99913	-119.76180	Ida Naughton	15.iv.19
INZ803	*Formica moki*	Santa Cruz Island	34.01710	-119.85844	Ida Naughton	12.iv.19
INZ805	*Formica moki*	Santa Cruz Island	34.01126	-119.81517	Ida Naughton	12.iv.19
INZ788	*Formica moki*	Santa Cruz Island	34.00149	-119.66800	Ida Naughton	22.vi.16
INZ806	*Formica moki*	Santa Cruz Island	34.02359	-119.87350	Ida Naughton	12.iv.19
INZ900	*Formica moki*	Santa Cruz Island	34.00077	-119.73560	Ida Naughton	12.iv.19
INZ901	*Formica moki*	Santa Cruz Island	33.82925	-119.64030	Ida Naughton	28.vii.19
INZ812	*Formica moki*	Santa Cruz Island	34.01256	-119.78147	Ida Naughton	12.iv.19
INZ813	*Formica moki*	Santa Cruz Island	33.99913	-119.76180	Ida Naughton	28.viii.16
INM902	*Formica moki*	Santa Cruz Island	33.99486	-119.63700	Ida Naughton	12.v.19
INZ845	*Dorymyrmex insanus*	Santa Cruz Island	33.98923	-119.67730	Ida Naughton	28.vii.19
INZ844	*Dorymyrmex insanus*	Santa Cruz Island	34.01244	-119.59597	Ida Naughton	12.v.19

INZ847	*Dorymyrmex insanus*	Santa Cruz Island	34.01546	-119.79753	Ida Naughton	28.vii.19
INZ843	*Dorymyrmex insanus*	Santa Cruz Island	33.99913	-119.76180	Ida Naughton	15.iv.19
INZ842	*Dorymyrmex insanus*	Santa Cruz Island	34.01244	-119.59597	Ida Naughton	12.v.19
INZ849	*Dorymyrmex insanus*	Santa Cruz Island	33.98923	-119.67730	Ida Naughton	27.vii.19
INZ852	*Dorymyrmex insanus*	Santa Cruz Island	33.99351	-119.63720	Ida Naughton	27.vii.19
INZ853	*Dorymyrmex insanus*	Santa Cruz Island	33.98923	-119.67730	Ida Naughton	28.vii.19
INZ850	*Dorymyrmex insanus*	Santa Cruz Island	34.00307	-119.61801	Ida Naughton	27.vii.19
INZ851	*Dorymyrmex insanus*	Santa Cruz Island	34.00990	-119.77178	Ida Naughton	28.vii.19
INZ848	*Dorymyrmex insanus*	Santa Cruz Island	34.01158	-119.69050	Ida Naughton	27.vii.19
INZ846	*Dorymyrmex insanus*	Santa Cruz Island	33.99817	-119.71370	Ida Naughton	29.vii.19
INM671	*Dorymyrmex insanus*	Lompoc Valley	34.68441	-120.42220	Ida Naughton	20.iv.19
INM673	*Dorymyrmex insanus*	Lompoc Valley	34.74174	-120.50670	Ida Naughton	21.iv.19
INM677	*Dorymyrmex insanus*	Lompoc Valley	34.72066	-120.46420	Ida Naughton	19.iv.19
INM674	*Dorymyrmex insanus*	Lompoc Valley	34.79786	-120.61470	Ida Naughton	20.iv.19
INM679	*Dorymyrmex insanus*	Lompoc Valley	34.72066	-120.46420	Ida Naughton	15.v.19
INM664	*Dorymyrmex insanus*	Lompoc Valley	34.61354	-120.55660	Ida Naughton	2.vi.19
INM666	*Dorymyrmex insanus*	Lompoc Valley	34.63170	-120.57583	Ida Naughton	2.vi.19
INM668	*Dorymyrmex insanus*	Lompoc Valley	34.75541	-120.58316	Ida Naughton	3.vi.19
INM669	*Dorymyrmex insanus*	Lompoc Valley	34.70408	-120.37616	Ida Naughton	3.vi.19
INM680	*Dorymyrmex insanus*	Lompoc Valley	34.72066	-120.46420	Ida Naughton	15.v.19
INM681	*Dorymyrmex insanus*	Lompoc Valley	34.74174	-120.50670	Ida Naughton	15.v.19
INM676	*Dorymyrmex insanus*	Lompoc Valley	34.79786	-120.61470	Ida Naughton	21.iv.19
INM682	*Dorymyrmex insanus*	Lompoc Valley	34.69746	-120.44398	Ida Naughton	15.v.19
INM621	*Tapinoma sessile*	Lompoc Valley	34.70511	-120.59870	Ida Naughton	24.iii.19
INM622	*Tapinoma sessile*	Lompoc Valley	34.74004	-120.57450	Ida Naughton	25.iii.19
INM623	*Tapinoma sessile*	Lompoc Valley	34.70511	-120.59870	Ida Naughton	24.iii.19
INM624	*Tapinoma sessile*	Lompoc Valley	34.73700	-120.56075	Ida Naughton	3.vii.19
INM615	*Tapinoma sessile*	Lompoc Valley	34.75541	-120.58316	Ida Naughton	3.vi.19
INM614	*Tapinoma sessile*	Lompoc Valley	34.71298	-120.47790	Ida Naughton	4.vii.19
INM617	*Tapinoma sessile*	Lompoc Valley	34.67641	-120.38703	Ida Naughton	3.vi.19
INM611	*Tapinoma sessile*	Lompoc Valley	34.68188	-120.43693	Ida Naughton	2.vii.19
INM639	*Tapinoma sessile*	Lompoc Valley	34.68188	-120.43693	Ida Naughton	31.vii.19
INM612	*Tapinoma sessile*	Lompoc Valley	34.73845	-120.56590	Ida Naughton	3.vii.19
INM619	*Tapinoma sessile*	Lompoc Valley	34.78385	-120.53050	Ida Naughton	19.iii.19
INM618	*Tapinoma sessile*	Lompoc Valley	34.68188	-120.43693	Ida Naughton	15.v.19
INM665	*Tapinoma sessile*	Lompoc Valley	34.63170	-120.57583	Ida Naughton	18.iii.19
INM620	*Tapinoma sessile*	Lompoc Valley	34.69746	-120.44398	Ida Naughton	18.iii.19
INZ768	*Tapinoma sessile*	Santa Cruz Island	34.00626	-119.75820	Ida Naughton	12.iv.19
INZ769	*Tapinoma sessile*	Santa Cruz Island	34.02359	-119.87350	Ida Naughton	12.iv.19
INZ764	*Tapinoma sessile*	Santa Cruz Island	33.99805	-119.72020	Ida Naughton	7.v.19
INZ766	*Tapinoma sessile*	Santa Cruz Island	34.00182	-119.86119	Ida Naughton	5.viii.16

INZ767	*Tapinoma sessile*	Santa Cruz Island	34.01158	-119.69050	Ida Naughton	15.iv.19
INZ772	*Tapinoma sessile*	Santa Cruz Island	34.01244	-119.59597	Ida Naughton	27.vii.19
INZ771	*Tapinoma sessile*	Santa Cruz Island	34.01204	-119.67850	Ida Naughton	27.vii.19
INZ770	*Tapinoma sessile*	Santa Cruz Island	34.01434	-119.79366	Ida Naughton	28.vii.19
INZ765	*Tapinoma sessile*	Santa Cruz Island	34.00397	-119.86119	Ida Naughton	5.viii.16
INM606	*Camponotus hyatti*	Lompoc Valley	34.74174	-120.50670	Ida Naughton	15.v.19
INM607	*Camponotus hyatti*	Lompoc Valley	34.71088	-120.43612	Ida Naughton	15.v.19
INM604	*Camponotus hyatti*	Lompoc Valley	34.71088	-120.43612	Ida Naughton	15.v.19
INM605	*Camponotus hyatti*	Lompoc Valley	34.74174	-120.50670	Ida Naughton	15.v.19
INM602	*Camponotus hyatti*	Lompoc Valley	34.67641	-120.38703	Ida Naughton	3.vi.19
INM600	*Camponotus hyatti*	Lompoc Valley	34.69746	-120.44398	Ida Naughton	2.vii.19
INM608	*Camponotus hyatti*	Lompoc Valley	34.69746	-120.44398	Ida Naughton	26.iii.19
INM609	*Camponotus hyatti*	Lompoc Valley	34.69746	-120.44398	Ida Naughton	26.iii.19
INM610	*Camponotus hyatti*	Lompoc Valley	34.72066	-120.46420	Ida Naughton	19.iv.19
INZ056	*Camponotus hyatti*	Santa Cruz Island	34.04678	-119.73750	Ida Naughton	29.vi.15
INZ827	*Camponotus hyatti*	Santa Cruz Island	34.00693	-119.76744	Ida Naughton	1.ix.16
INZ091	*Camponotus hyatti*	Santa Cruz Island	34.05000	-119.87060	Ida Naughton	1.vi.14
INZ094	*Camponotus hyatti*	Santa Cruz Island	34.00306	-119.67640	Ida Naughton	2.vi.14
INZ095	*Camponotus hyatti*	Santa Cruz Island	33.99944	-119.66920	Ida Naughton	4.iv.14
INZ840	*Camponotus hyatti*	Santa Cruz Island	34.00990	-119.77178	Ida Naughton	12.iv.19
INZ023	*Camponotus hyatti*	Santa Cruz Island	33.99941	-119.72760	Ida Naughton	vi.10.14
INZ835	*Camponotus hyatti*	Santa Cruz Island	34.01710	-119.85844	Ida Naughton	12.iv.19
INZ836	*Camponotus hyatti*	Santa Cruz Island	34.01256	-119.78147	Ida Naughton	12.iv.19
INZ837	*Camponotus hyatti*	Santa Cruz Island	34.00626	-119.75820	Ida Naughton	12.iv.19
INZ830	*Camponotus hyatti*	Santa Cruz Island	34.01126	-119.81517	Ida Naughton	16.iii.19
INZ831	*Camponotus hyatti*	Santa Cruz Island	33.99913	-119.76180	Ida Naughton	14.iii.19
INZ300	*Camponotus hyatti*	Santa Cruz Island	34.00307	-119.61801	Ida Naughton	31.v.17
INZ036	*Camponotus hyatti*	Santa Cruz Island	34.00110	-119.75160	Ida Naughton	vi.10.14

Table 3-S2. Trimmed read count metrics for NovaSeq data.

Sample ID	number of reads	total bp	mean length	95 CI lengtl	minimum length	maximum length
INM611	4749121	700346132	147.4685804	0.00704398	40	151
INM612	5987684	884636757	147.7427261	0.00589089	40	151
INM614	3467033	514625662	148.4340247	0.00699667	40	151
INM615	8291915	1229772477	148.3098267	0.00464233	40	151
INM617	7482611	1108253495	148.1105319	0.00502231	40	151
INM618	5912890	875609602	148.0848793	0.00564028	40	151
INM619	4789201	709822144	148.2130618	0.00620589	40	151
INM620	5428248	803492420	148.0205805	0.00608882	40	151
INM621	4952627	734002560	148.2046922	0.00605755	40	151
INM622	4281342	630599363	147.2901167	0.00711854	40	151
INM623	3377529	500729145	148.2531001	0.0073259	40	151
INM624	6671045	988017971	148.1054274	0.00541801	40	151
INM625	4835864	715974701	148.0551771	0.00647276	40	151
INM626	4488740	663773532	147.8752461	0.00690302	40	151
INM627	3400665	501786294	147.555344	0.00832593	40	151
INM628	6826577	1011978663	148.2410091	0.00526213	40	151
INM631	9883938	1463707358	148.0894921	0.00449632	40	151
INM632	6390068	946416818	148.1074721	0.00556547	40	151
INM633	5124383	756518864	147.6312102	0.0067152	40	151
INM636	3036776	448804819	147.7898992	0.00853443	40	151
INM637	3036776	448804819	147.7898992	0.00853443	40	151
INM639	3909895	578820470	148.0399013	0.00721416	40	151
INM640	7624416	1126957536	147.8090304	0.00530395	40	151
INM641	5833440	857836667	147.0550253	0.00671988	40	151
INM642	8199475	1206612303	147.1572635	0.0056076	40	151
INM643	4430600	653415680	147.4779217	0.00736911	40	151
INM644	4034383	586791738	145.4477024	0.01020019	40	151
INM645	2929914	428999668	146.4205666	0.00945362	40	151
INM646	7355888	1092376394	148.5036741	0.00475987	40	151
INM647	4411815	655757004	148.6365598	0.00585525	40	151
INM648	7564524	1123785725	148.5600052	0.00465178	40	151
INM650	5602801	827828180	147.7525581	0.00626473	40	151
INM651	9017516	1336005451	148.1567042	0.00458361	40	151
INM652	7850606	1163161149	148.1619571	0.00499175	40	151
INM653	10163086	1501669247	147.7572114	0.00468172	40	151
INM654	4970968	738473874	148.5573582	0.0057105	40	151
INM655	7255160	1077511997	148.5166415	0.0048511	40	151
INM656	4301946	638825503	148.496867	0.00620173	40	151
INM657	4136813	614496146	148.5433705	0.00622593	40	151
INM659	4577499	679887653	148.528193	0.0057284	40	151
INM660	7724891	1149595906	148.817104	0.00440313	40	151
INM661	7182005	1067582801	148.646903	0.00462184	40	151
INM662	4861690	722121242	148.532967	0.00585952	40	151
INM664	4855719	719295268	148.133627	0.00603369	40	151
INM665	9769170	1441151951	147.520409	0.00485072	40	151
INM666	5003474	739684473	147.834179	0.00651966	40	151
INM668	6776491	1005434138	148.3709103	0.00498123	40	151
INM669	5189756	768350607	148.0513934	0.00592993	40	151
INM671	4793978	706850111	147.4454224	0.00627231	40	151
INM673	5411725	802935821	148.3696642	0.00562728	40	151
INM674	4102061	606702668	147.9019127	0.00653235	40	151
INM676	6472742	958239847	148.0423362	0.00519194	40	151
INM677	4949830	732509158	147.9867305	0.00589041	40	151
INM679	5180603	768283523	148.3000189	0.00573919	40	151
INM680	4250199	630019688	148.2329858	0.0065711	40	151
INM681	4820670	712236088	147.7462859	0.00655492	40	151
INM682	5022977	744164376	148.1520572	0.00582333	40	151
INM705	4972432	737014682	148.2201631	0.00615384	40	151
INM707	13751201	2043075908	148.5743615	0.00346855	40	151
INM708	6584348	976766632	148.3467508	0.00524974	40	151
INM709	6491206	961713653	148.1563908	0.00546115	40	151
INM710	2881470	424766484	147.4131204	0.0092658	40	151
INM711	5642117	834365076	147.8815622	0.00609962	40	151
INM712	4267290	630982126	147.8648337	0.00709879	40	151
INM713	8173752	1210371676	148.0803034	0.00492609	40	151
INM714	3570148	529071715	148.1932164	0.00721714	40	151
INM715	7377633	1088434217	147.5316293	0.00567678	40	151
INM716	14358675	2129646119	148.3177326	0.00357141	40	151
INM717	7936569	1174351816	147.9671904	0.005097	40	151
INM718	10385609	1540137203	148.2953193	0.00421537	40	151
INM720	5931534	878053446	148.0314276	0.00583328	40	151
INM722	13156456	1948248927	148.0831105	0.00388935	40	151
INM728	6104706	899530084	147.3502711	0.00641275	40	151
INM729	6227371	924508633	148.458898	0.00529402	40	151
INM730	11057834	1631690858	147.559717	0.00462292	40	151
INM731	6810553	1006430223	147.775111	0.00571237	40	151
INM732	1350234	197901444	146.5682571	0.01388491	40	151

Sample ID	number of reads	total bp	mean length	95 CI length	minimum length	maximum length
INM735	6560818	970696661	147.9536029	0.005654514	40	151
INM737	9596937	1416785829	147.62896	0.0048074	40	151
INM892	4579066	679962373	148.4936826	0.006144165	40	151
INM894	17953858	2652792787	147.7561417	0.003521663	40	151
INM899	5408266	798280069	147.6036994	0.006279217	40	151
INM900	4366042	647208505	148.236894	0.006617604	40	151
INM901	3387260	502298282	148.2904418	0.007436076	40	151
INM902	8977165	1324354403	147.5247924	0.005169949	40	151
INM903	5958146	880965195	147.8589472	0.005921939	40	151
INM904	2404531	353880744	147.1724607	0.010375886	40	151
INM905	3738541	552578294	147.805867	0.007635132	40	151
INZ738	5261930	783040457	148.812405	0.00530054	40	151
INZ739	5505977	818010659	148.567758	0.00537376	40	151
INZ746	5427140	807388339	148.7686588	0.005171793	40	151
INZ747	6837270	1015292767	148.4938824	0.004927544	40	151
INZ748	3885290	577303457	148.586967	0.006414755	40	151
INZ749	11177602	1661223285	148.6207225	0.003658351	40	151
INZ750	4776356	710416262	148.7360368	0.005613414	40	151
INZ751	4523505	672668881	148.7052365	0.00573342	40	151
INZ752	5078499	755029623	148.671807	0.00558994	40	151
INZ753	5616471	832896620	148.2953655	0.005741355	40	151
INZ755	2940963	435249923	147.995715	0.00845998	40	151
INZ757	13163324	1949233525	148.080646	0.00390337	40	151
INZ758	5164888	764347061	147.989087	0.00639044	40	151
INZ759	12779452	1892587214	148.096117	0.00393332	40	151
INZ760	8738875	1299264290	148.676379	0.00422468	40	151
INZ764	3475374	515532310	148.338657	0.00715673	40	151
INZ765	3689584	545917478	147.9617968	0.007367537	40	151
INZ766	3830745	567258215	148.0803904	0.007203935	40	151
INZ767	2528459	373986421	147.9108109	0.008972867	40	151
INZ768	4181684	619369034	148.1147389	0.006741548	40	151
INZ769	6323077	935419734	147.9374257	0.005583663	40	151
INZ770	4750276	702860835	147.9621047	0.006567528	40	151
INZ771	4370563	647248378	148.0926778	0.006753578	40	151
INZ772	9159905	1356377571	148.0776898	0.004639288	40	151
INZ785	4221254	626248074	148.3559326	0.006620477	40	151
INZ787	9774351	1446683381	148.0081267	0.004605413	40	151
INZ788	3331732	494910494	148.544509	0.007204339	40	151
INZ800	4419676	653894195	147.950708	0.00691875	40	151
INZ803	8639549	1284385029	148.6634347	0.004350318	40	151
INZ805	4182352	621922420	148.7015966	0.006208295	40	151
INZ806	3855442	573822124	148.8343292	0.006272389	40	151
INZ812	4182352	621922420	148.7015966	0.006208295	40	151
INZ813	3855442	573822124	148.8343292	0.006272389	40	151
INZ815	8119810	1196910841	147.4062621	0.005440611	40	151
INZ816	3828748	560421878	146.3720981	0.008923171	40	151
INZ817	6633858	972144222	146.5428145	0.006119293	40	151
INZ818	2205585	307582836	139.456351	0.018019443	40	151
INZ819	6412171	944924655	147.364232	0.00601122	40	151
INZ820	4817953	712295536	147.8419437	0.006670641	40	151
INZ821	5624016	830036700	147.587898	0.006192552	40	151
INZ822	6141641	906518326	147.6019725	0.006114859	40	151
INZ825	6283853	926687297	147.4711928	0.006116974	40	151
INZ826	2099970	307228890	146.3015615	0.01166023	40	151
INZ842	5446047	807946631	148.354693	0.005564585	40	151
INZ843	3230444	478990698	148.2739518	0.007279964	40	151
INZ844	4239998	629828937	148.5446307	0.00610848	40	151
INZ845	4936393	732801675	148.4488117	0.005797713	40	151
INZ846	3174658	470513032	148.2090455	0.00736611	40	151
INZ847	3730228	550181746	147.4927929	0.007011842	40	151
INZ848	4649109	688095806	148.0059525	0.006227945	40	151
INZ849	8952279	1328688640	148.4190383	0.004398999	40	151
INZ850	9908900	1471537360	148.5066314	0.004111645	40	151
INZ851	4386110	650155200	148.2304821	0.006518273	40	151
INZ852	4640313	688256444	148.3211249	0.006249687	40	151
INZ853	7870732	1168101331	148.4107617	0.0045692	40	151
INZ855	5670272	837788643	147.7510502	0.006264628	40	151
INZ856	5006213	741791425	148.1741638	0.006210555	40	151
INZ857	3074005	455027645	148.0243672	0.00813752	40	151
INZ858	2854206	422657065	148.0821864	0.008405844	40	151
INZ859	3512357	518423908	147.6000042	0.008135497	40	151
INZ860	3398527	502903379	147.9768673	0.007819379	40	151
INZ861	5656796	838007822	148.1417788	0.005894696	40	151
INZ862	4568184	675694238	147.9130959	0.006814039	40	151
INZ863	6762409	999537706	147.8079344	0.005695448	40	151
INZ864	7640978	1129531420	147.8255035	0.005341426	40	151
INZ866	3578990	529048663	147.8206597	0.007807838	40	151
INZ868	4201286	622838989	148.2496048	0.006712241	40	151
INZ869	6002907	888668657	148.0397176	0.005810459	40	151
INZ873	3414273	505867296	148.1625213	0.007552001	40	151
INZ874	3442787	510004148	148.137003	0.007562548	40	151
INZ875	3466319	512826235	147.9454819	0.007779282	40	151
INZ877	6129106	908568383	148.2383211	0.005548413	40	151
INZ878	7952784	1179181210	148.2727571	0.00483682	40	151
INZ879	6083865	901941125	148.2513378	0.005559977	40	151
INZ880	6842818	1012347797	147.9431131	0.005504373	40	151
INZ883	5509440	814267020	147.7948793	0.006330624	40	151
INZ885	7583616	1124476614	148.2771034	0.004929092	40	151
INZ886	8782799	1303730719	148.4413703	0.004429382	40	151
INZ887	6345876	941961633	148.4368168	0.005265655	40	151

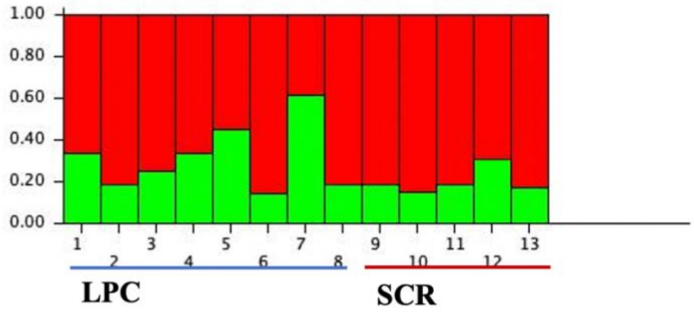
Table 3-S3. Ant gyne morphological measurements. All measurements are in millimeters.

Species	Weber's Length	Wing Length	Head Width	Ratio Wing Length / Weber's Length
Formica moki	3.50	8.76	1.82	2.50
Dorymyrmex insanus	1.39	3.80	0.74	2.73
Prenolepis imparis	3.17	8.76	1.40	2.76
Pheidole hyatti	2.29	6.80	1.48	2.96
Crematogaster marioni	2.43	6.69	1.60	2.75
Camponotus hyatti	3.25	9.40	1.80	2.89
Solenopsis molesta	1.21	3.65	0.74	3.01
Monomorium ergatogyna	1.50	3.67	0.66	2.45
Tapinoma sessile	1.35	3.32	1.05	2.46

Table 3-S4. The number of aligned UCE loci (complete dataset) for each species used for calculating the genetic diversity metrics Tajima's D, Watterson's θ, and nucleotide diversity.

Species	**Number of aligned UCEs**
Formica moki	934
Dorymyrmex insanus	634
Prenolepis imparis	696
Pheidole hyatti	1134
Crematogaster marioni	766
Camponotus hyatti	815
Solenopsis molesta	686
Monomorium ergatogyna	1392
Tapinoma sessile	865

Figure 3-S1. STRUCTURE plot for *Solenopsis molesta* at K=2, based on 1975 SNPS.



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