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Environmental determinants of  $\delta^{15}\text{N}$  of ants on Santa Cruz Island

A thesis submitted in partial satisfaction of the requirements for the degree Master of  
Science

in

Biology

by

Edward Yiyen Chen

Committee in Charge:

Professor David Holway, Chair  
Professor James Nieh, Co-Chair  
Professor Carolyn Kurle

2021

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University of California San Diego

2021

## TABLE OF CONTENTS

Thesis Approval Page.....	iii
Table of Contents.....	iv
List of Figures.....	v
List of Tables.....	vi
Acknowledgments.....	vii
Abstract of the Thesis.....	viii
Chapter 1 ... ..	1
Appendix.....	17
References.....	18

## LIST OF FIGURES

Figure 1 Map of the 18 long term control and experimental plots on Santa Cruz Island.....	12
Figure 2 Correlation matrix showing Pearson’s correlation coefficients between each environmental variable.....	12
Figure 3 Map of $\delta^{15}\text{N}$ of plants relative to a Digital Elevation Model on Santa Cruz Island.....	13
Figure 4 Map of $\delta^{15}\text{N}$ of soil relative to a Digital Elevation Model on Santa Cruz Island .....	13
Figure 5 Linear regression of soil $\delta^{15}\text{N}$ predicting plant $\delta^{15}\text{N}$ . Line shows significant least square regression .....	14
Figure 6 $\delta^{15}\text{N}$ values for seven native ant species on control plots in 2017 and 2019.....	14
Figure 7 Corrected $\delta^{15}\text{N}$ of seven native ant species compared between experimental and control plots .....	15
Figure 8 Species richness of native ants on experimental and control plots .....	15

## LIST OF TABLES

Table 1 List of the twelve species and their aliases identified and sampled from in 2017 and 2019.....	16
Table A1 Invasion year, GPS coordinates, elevation, distance from shore, sampling year, and treatment year of the 18 long term study plots.....	17

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## ABSTRACT OF THE THESIS

Environmental determinants of  $\delta^{15}\text{N}$  of ants on Santa Cruz Island

by

Edward Yiyen Chen

Master of Science in Biology

University of California San Diego, 2021

Professor David Holway, Chair  
Professor James Nieh, Co-Chair

Invader-removal experiments can lend insight into the ecological resilience of biological assemblages and the extent to which they can recover from perturbations. Argentine ant invasions on Santa Cruz Island have disrupted the diversity and functionality of ant assemblages. This thesis sought to quantify changes in native ant species following invader removal in nine experimental plots paired with nine control plots on Santa Cruz Island. Stable isotope analysis (variation in  $\delta^{15}\text{N}$ ) was used to

estimate relative trophic positions of and resource acquisition by native ant species. Spatiotemporal variation in  $\delta^{15}\text{N}$  was also investigated to assess its relative impact on the trophic niches of twelve native ant species. Stable isotope analysis was conducted on an assemblage of native ants in 2017 and 2019 following the removal of the Argentine ant from Santa Cruz Island conducted by The Nature Conservancy with support from the National Park Service. Soil  $\delta^{15}\text{N}$  and plant  $\delta^{15}\text{N}$  values were positively related to one another. Subsequently, this correlation was used to correct for the  $\delta^{15}\text{N}$  values of native ant species.  $\delta^{15}\text{N}$  values for native ant species did not differ between control and experimental plots. Native ant species also displayed temporal constancy in  $\delta^{15}\text{N}$  values in 2017 and 2019. Overall, there was significant variation in trophic positions among native ant species. It is hypothesized that functional traits of the ant species played a role in niche diversification, and overall competition levels were minimized as a result of these differences. Species richness was lower on experimental plots as the experimental recovery is still ongoing, and additional ant species are expected to re-colonize the plots. The similar trophic positions of ants on invaded and uninvaded plots demonstrated the ability of native ants to recover to their pre-invasion state following successful eradication of the invader.

## CHAPTER 1

### Introduction

Ecological resilience describes the ability of biological systems to return to former configurations following disturbances (Briske et al. 2017, Gunderson 2000, Hollings 1973). Such disturbances can include abiotic factors such as environmental fluctuations and destructive events (Pickett and White 1985). Disturbances can also include biotic factors such as invasive species that have the potential to disrupt ecosystems (DeAngelis and Waterhouse 1987). Biological invasions can be defined as the spread of an introduced taxon in a region (Richardson et al. 2000). Invasive species impact native communities by displacing native species, altering functionalities of native species, as well as altering nutrient dynamics (Menke et al. 2010, Yelenik and Antonio 2013, Vander Zanden et al. 2004).

The Argentine ant (*Linepithema humile*) has been the focus of previous studies on biological invasion and ecological resilience (Holway et al. 2002, Naughton et al. 2020). Argentine ants were first detected in California in 1907 and have been introduced on half of the California Channel Islands including Santa Cruz Island (Boser et al. 2014). Santa Cruz Island is host to 33 different species of native ants, but these species are at risk of decline due to invasion by the Argentine ant (Boser et al. 2017, Menke et al. 2018, Naughton et al. 2020). The success of the Argentine ant can in part be attributed to its aggression and its competitive edge in resource discovery and abundance (Menke et al. 2018). The abundance of this species further contributes to its competitive dominance, and such competition can be a cause of compositional changes in native assemblages. (Firn et al. 2010, Krushelnycky et al. 2009, Yelenik and Antonio 2013). Argentine ant invasions also have social and economic impacts as they are a household nuisance, and can cause productivity losses in agriculture (Ward et al. 2010).

Evaluating the effects of removing introduced species, such as the Argentine ant in the context of environmental factors can better inform management practices as well as elucidate the mechanisms of ecological resilience (Kumschick et al. 2014). Such analyses can also reveal how much of the native species' compositional changes can be attributed to the Argentine ant invasion (Kumschick et al. 2014). Changes in native species composition can alter a species' functionality and ecological role especially in relation to a food web (Philpott and Armbrecht 2006). The food web is structurally characterized by trophic interactions that are determinants of energy flow through an ecosystem (Gibb and Cunningham 2013).

Trophic interactions can be used as a functional index of ecological resilience as they can indicate how well the structural processes of the ecosystem are maintained or recovered (Briske et al. 2017, Vander Zanden et al. 1999). To study trophic interactions has not been an easy task (Fry 2006). However, with the introduction of stable isotope analysis, one can characterize an animal's diet using the ratio of heavy to light isotopes such as nitrogen present in its tissue (Cabana and Rasmussen 1996, Peterson and Fry 1987, Tillberg et al. 2006). This thesis aims to use stable isotope analysis to investigate whether or not native ants re-colonizing formerly invaded areas on Santa Cruz Island have shifted their diets, and thus trophic positions after experimental removal of Argentine ants.

The ratio of nitrogen isotopes (e.g.,  $\delta^{15}\text{N}$ ) allows for the determination of the relative trophic positions and could provide evidence for changes in the trophic function as result of the invasion (Layman et al. 2007).  $\delta^{15}\text{N}$  values can also indicate niche breadth and variation as a result of competition between species (Layman et al. 2007). Re-colonization of native ant assemblages and information on trophic positions can shed light on how well native ants recover from or persist functionally in the face of a biological disturbance. This thesis will also take into account abiotic factors that can potentially influence the trophic positions and diets of the native ant assemblages. Due to the spatial variation of the different sampling locations, there can be inherent variation in the

soil and vegetation that can play part in shaping the ants' diets (Brown et al. 2013, Eddy 2009).

Temporal variation perhaps caused by year-to-year variation in rainfall will also be investigated as a potential factor shaping variation in resource acquisition.

Based on community assembly theory, there are several possible outcomes of re-colonization after invader removal. Firstly, reassembly could show evidence of an alternate stable state in which the community structure does not return to pre-removal configurations, but a complete turnover of individuals that could persist is established due to a different colonization history (Beisner et al. 2003, Schröder et al. 2005). Alternate stable states are more likely when there is environmental similarity, a larger regional species pool, high connectivity, low productivity and low disturbance (Chase 2003, Connell and Sousa 1983, Fukami and Nakajima 2011). Priority effects may also be present, in which the establishment of the first colonizing species could affect the establishment of later arriving species by monopolizing resources (Symons and Arnott 2014). This process could cause one species to become more dominant after community reassembly as the niche difference is too small to permit co-existence (Blaustein and Margalit 1996, Chen et al. 2020, Fukami et al. 2016).

Here, it is predicted that native ants would most likely be able to re-colonize and recover their previous trophic functions and assemblage composition following successful eradication of the invader, if the environmental conditions remain similar (Weiher et al. 2011). Previous studies have demonstrated success in native ant recovery after invader removal, which could substantiate the effectiveness of invasive pest removal efforts (Cook et al. 2003, Gaigher et al. 2012, Hanna et al. 2015). The differences in mean  $\delta^{15}\text{N}$  values between experimental and control ant assemblages will be tested in context of environmental factors to see the extent of recovery. Complete recovery to pre-invaded trophic functions could give insight into the resilience of the native ant community on Santa Cruz Island.

## Methods

### *Study System*

Sampling was conducted on Santa Cruz Island, the largest of the eight California Channel Islands off the coast of southern California, USA. Santa Cruz Island (249 km<sup>2</sup> and 30km offshore) supports an ant fauna of 33 native ant species that is comparable in many respects to the diversity on the mainland (Miller 2000). Beginning in 2010, nine control plots (never invaded or treated), and nine experimental plots (invaded and treated) were established on Santa Cruz Island (Figure 1). The plots conformed to a replicated, before-after, control-impact paired series (BACIPS) design spatially distributed inside and outside of multiple Argentine ant infestation sites. Each plot is a 10-m radius circle (314m<sup>2</sup>) placed within a continuous island scrub oak (*Quercus pacifica*) habitat. All plots were similar with respect to terrain and habitat attributes, and placed between 100m to 1km from each other.

### *Data collection*

The Nature Conservancy conducted eradication protocols on four major Argentine ant infestation sites between 2012 and 2016 (Boser et al. 2014, Boser et al. 2017). Data for this paper were collected during the field seasons of 2017 and 2019. Field-work in 2017 sampled native ants on control plots 1-9, as well as on five supplemental plots that were sampled only in some years. Field-work in 2019 sampled native ants on long-term control (uninvaded) and experimental (treated) plots, as well as soil, and plants from the same plots. Twelve ant species were identified and sampled in these two years and are listed in Table 1. GPS coordinates, invasion and treatment year, sampling initiation year are listed in Appendix 1.

Ant specimens were collected using aspirators and placed into a vial, then into a 0°C freezer all within one hour of sample collection. The samples were kept frozen for at least four hours before processing. For the ants, the post-petiole, petiole and gaster were removed because these body parts

contained recently digested food that may distort the actual nitrogen stable isotope ratio in ants (Tillberg et al. 2006). All ant specimens were dried for three hours at 70°C, then stored in 55 x 91 mm Bioquip End-Opening Glassine Envelopes with added ¼ cup of Bioquip Products Indicating Silica Gel as desiccant (Smith and Suarez 2010). A mass of 0.5-1.5 mg of each sample was packed into Costech 5 x 9 mm tin capsules and sent to the University of California Davis Stable Isotope Facility where samples were analyzed with a Europa-Hydra 20/20 continuous flow Isotope Ratio Mass Spectrometer.

All stable isotope values are reported in delta notation where  $\delta = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$ , with units expressed in ‘‰’ or ‘permil’ (Fry 2006).  $R_{\text{sample}}$  is the ratio between the heavy and light isotopes of an element, which in the case of nitrogen is  $^{15}\text{N}: ^{14}\text{N}$  (Fry 2006). Stable isotope ratios are compared to an internationally used standard for heavy to light isotope ratios ( $R_{\text{standard}}$ ), which in the case of nitrogen is derived from the air in the atmosphere (Fry 2006).  $\delta^{15}\text{N}$  can give an approximation of the relative trophic position of each ant because nitrogen values of consumers are typically enriched relative to their diets (Fry 2006, Tillberg et al. 2006). Any change in the stable isotope ratio is known as fractionation. Typically, an increase in one trophic level is characterized by an enrichment of 3.4‰ in the  $\delta^{15}\text{N}$  value (Fry 2006, Tillberg et al. 2006).

### *Statistical analysis*

To ensure that plot assignments were randomized with respect to environmental variation, paired *t*-tests were conducted for soil  $\delta^{15}\text{N}$  on invaded and uninvaded plots ( $t = 0.77$ ,  $P = 0.46$ ) as well as for plant  $\delta^{15}\text{N}$  on invaded and uninvaded plots ( $t = -1.48$ ,  $P = 0.21$ ). To examine relationships among environmental factors (soil and plants) and geographic attributes, Pearson’s correlations were conducted to see how elevation and distance from shore associated with soil  $\delta^{15}\text{N}$  and plant  $\delta^{15}\text{N}$  values averaged per plot (Figure 2). Because only soil  $\delta^{15}\text{N}$  was significantly correlated with plant

$\delta^{15}\text{N}$  ( $r=0.68$ ,  $P < 0.05$ ), a univariate regression was used to test the relationship between soil and plant  $\delta^{15}\text{N}$  values to determine if plant  $\delta^{15}\text{N}$  can be predicted from soil  $\delta^{15}\text{N}$ . The elevation above sea level and distance from shore for each plot were extracted from the geographic coordinates using ArcGIS Pro (Esri Inc.) and are also included in Appendix 1.

To test for temporal variation in  $\delta^{15}\text{N}$  values, all ant species collected from control plots in 2017 and 2019 were compared. Interspecific variation in  $\delta^{15}\text{N}$  values within the native assemblages was also taken into consideration. Thus, a linear mixed effects model was conducted on raw  $\delta^{15}\text{N}$  values of ants with year and ant species treated as fixed effects, and plot pair as a random effect to account for the inherent variation among the different plots.

Given the relationship between the environmental factors, the assimilated nitrogen in plant resources taken up by the ants was accounted for. Thus, all  $\delta^{15}\text{N}$  values of the ants in 2019 for subsequent analyses were corrected by subtracting the  $\delta^{15}\text{N}$  values of the plants from that of the ants (ants  $\delta^{15}\text{N} - \text{plants } \delta^{15}\text{N}$ ) measured on the same plots (Cronin et al. 2015). This approach allows for calibration of the baseline  $\delta^{15}\text{N}$  of the ants and allows for comparison across plot types (Cronin et al. 2015). Another linear mixed effects model was used on the corrected  $\delta^{15}\text{N}$  values of the ants with plot type (experimental or control) and species as fixed effects, and plot number as random effects to see whether variation in plot type or species is contributing to the variation  $\delta^{15}\text{N}$  values. Both linear mixed effects models were also tested for suitability by examining the normality of residuals.

One-sample  $t$ -tests were used to compare the distribution of ant  $\delta^{15}\text{N}$  values on control plots to the mean  $\delta^{15}\text{N}$  values of the ants on experimental plots at the species level in 2019. One sample  $t$ -tests were conducted on five species: *Camponotus hyatti*, *Camponotus maritimus*, *Formica moki*, *Monomorium ergatogyna*, and *Pheidole hyatti*. A Bartlett's test of variance was conducted on the same five species (*C. hyatti*, *C. maritimus*, *F. moki*, *M. ergatogyna*, *P. hyatti*) to see if there were differences in variance in the  $\delta^{15}\text{N}$  values of ants on control and experimental plots that could



indicate changes in diet breadths of the ants due to resource partitioning as a result of competition. Variance could also indicate the ants' abilities to occupy and maintain multiple positions on a food web.

To analyze changes in native ant species richness, a Kruskal-Wallis Chi-squared test was used to assess the difference in the number of species between control and experimental plots in 2019. All statistical tests and visualizations were performed in R and Python.

## Results

Pearson's correlations were performed to analyze relationships between soil, plants, elevation, and distance from shore to delineate a possible environmental gradient that underlies the spatial variation of nitrogen isotopes on Santa Cruz Island. Figure 3 displays a map of the spatial distribution of the plant  $\delta^{15}\text{N}$  values relative to a digital elevation model of Santa Cruz Island, and Figure 4 displays a map of the spatial distribution of the soil  $\delta^{15}\text{N}$  values relative to a digital elevation model of Santa Cruz Island.

For the data collected in 2019, there was no significant association between plant  $\delta^{15}\text{N}$  values and elevation ( $r = 0.12$ ,  $P = 0.72$ ) or distance from shore ( $r = -0.49$ ,  $P = 0.12$ ). Pearson's correlation also revealed that soil  $\delta^{15}\text{N}$  values had no significant associations with elevation ( $r = 0.56$ ,  $P = 0.07$ ) or distance from shore ( $r = -0.56$ ,  $P = 0.07$ ). The univariate linear regression revealed that soil  $\delta^{15}\text{N}$  values predicted plant  $\delta^{15}\text{N}$  values with a significant positive relationship (Fig. 5;  $df = 1$ ,  $R^2 = 0.46$ ,  $F = 7.75$ ,  $P < 0.05$ ).

A linear mixed effects model was conducted on the different ant species on control plots in 2017 and 2019 with  $\delta^{15}\text{N}$  values as the dependent variable. There were seven species on control plots with sufficient data in both 2017 and 2019 (Fig. 6). The linear mixed effects model revealed that the  $\delta^{15}\text{N}$  values of native ant assemblages on control plots did not differ significantly between 2017 and 2019 ( $P = 0.17$ ), but there was significant variation in  $\delta^{15}\text{N}$  values among each species ( $P < 0.01$ ).

$\delta^{15}\text{N}$  values of native ant species colonizing experimental plots generally resembled those of native ants on control plots (Fig. 7). The linear mixed effects model showed that there was no significant variation in  $\delta^{15}\text{N}$  values across plot types ( $P = 0.40$ ) but species again differed from one another ( $P < 0.01$ ).

For all five species tested, ants colonizing experimental plots did not differ from those on control plots: *C. hyatti* ( $t = -0.17$ ,  $P = 0.87$ ), *C. maritimus* ( $t = 0.20$ ,  $P = 0.85$ ), *F. moki* ( $t = 0.37$ ,  $P = 0.72$ ), *M. ergatogyna* ( $t = 1.37$ ,  $P = 0.21$ ), *P. hyatti* ( $t = 1.20$ ,  $P = 0.26$ ). The same five species were tested for differences in variance with the Bartlett's test but did not show significant differences in  $\delta^{15}\text{N}$  variance between control and experimental plots: *C. hyatti* ( $P = 0.35$ ), *C. maritimus* ( $P = 0.92$ ), *F. moki* ( $P = 0.92$ ), *M. ergatogyna* ( $P = 0.37$ ), and *P. hyatti* ( $P = 0.72$ ).

In terms of species richness estimates from 2019, there was a lower species richness overall on the experimental plots compared to that of control plots (Fig. 8;  $H(1) = 5.43$ ,  $P < 0.01$ ). The median species richness for the experimental plots was four species compared to a median of 6.5 species on the control plots. However, the native assemblages on experimental plots are still in the process of re-colonization after the invader removal.

## Discussion

The environmental data revealed uniformity in the soil and plant  $\delta^{15}\text{N}$  values across elevation on Santa Cruz Island. However, soil  $\delta^{15}\text{N}$  values contributed to plant  $\delta^{15}\text{N}$  values that are the main resources (directly and indirectly) taken up by the ants. The uniformity in soil  $\delta^{15}\text{N}$  values across the island rules out environmental heterogeneity as a confounder of variation in ant  $\delta^{15}\text{N}$  values (Ohdo and Takahashi 2020).

The results also demonstrated that the raw  $\delta^{15}\text{N}$  values of each native ant species on the control plots are comparable between 2017 and 2019. This temporal constancy can be reflective of the steady state that the native ant assemblages have achieved over time in the absence of a biological invasion

(Hulvey and Aigner 2014, Lengyel et al. 2015). This result could also indicate that resources assimilated by ants do not vary much from year to year. Thus, temporal changes can be ruled out as being a relevant factor in shaping resources up-taken by each ant species (Correa and Winemiller 2014).

Significant variation in the  $\delta^{15}\text{N}$  values among native ant species was evident on the control plots. These interspecific differences can indicate interspecific variation in trophic niches occupied by the ants (Raffard et al. 2020). Trophic niches can be shaped by environmental, physiological and biotic factors such as competition. Two types of niches can determine the structure of community assembly: the fundamental and realized niche (Chase 2011). The fundamental niche predicts whether a species can persist in a given habitat based on the environmental characteristics and functional traits of the species (Anderson et al. 2002, Kraft et al. 2015, Tingley et al. 2014). The realized niche typically is a restrained fundamental niche in which there are biotic factors imposed on the species including competitors, mutualists, and consumers that more accurately reflect the actual distribution of the species (Begley-Miller et al. 2014).

Some studies have shown that diet variation is what contributes most to niche partitioning between species (Nakano et al. 1999, Van der Zanden et al. 2000). Ants could partition their resources by foraging for different types of food based on body size variation and different energetic requirements (Cloyed et al. 2017, Raffard et al. 2020, Zhao et al. 2014). Previous morphological analyses have mentioned that *M. ergatogyna*, *P. hyatti*, *T. sessile* are known to be more carnivorous in diet that could explain their higher mean  $\delta^{15}\text{N}$  values (Dowd and Kok 1981, Schat 2018). A previous study has shown that *M. ergatogyna* and *P. hyatti* have smaller bodies, and larger cranial features that could predict higher  $\delta^{15}\text{N}$  values, and thus trophic levels (Schat 2018). Given that the environmental heterogeneity has been corrected for, functional traits are more likely to give rise to variation in resource acquisition in ants that contribute to resource partitioning (Kotler and Brown

1988). However, individual diet sources are hard to track, and post-hoc analyses will be needed to see which morphological features contribute more to resource partitioning. Regardless, this species-level niche variation could be the mechanism promoting coexistence among different ant species while minimizing competition (Clark et al. 2007, Roeder and Kaspari 2017).

On the other hand, the one-sample *t*-tests indicated that each native ant species that are recolonizing experimental removal plots closely resembled those on control plots with respect to their  $\delta^{15}\text{N}$  values. The linear mixed effects model substantiated this finding by showing that the overall variation in the  $\delta^{15}\text{N}$  values was among the different species present, and not attributed to the plot types (experimental or control). The presence, and similarities of trophic levels of ants on experimental plots are indicative of a successful recovery of native ant assemblages to their pre-invaded state following invader removal. Their presence is also representative of the ants' realized niches (Torres-Campos et al. 2020). Given their habitat and functional attributes, each native ant species adapted to a specialized trophic function in the presence of other species as evident in their different  $\delta^{15}\text{N}$  values (Goldberg et al. 1999, Pontarp and Petchey 2016). Similar variances in ant  $\delta^{15}\text{N}$  values across plot types could indicate similar diet breaths of ants colonizing experimental and control plots (Bertness and Callaway 1994, Weiher et al. 2011, Weiher et al. 1998). The recolonization abilities of the native ants may be a result of a high regional species pool and relatively stable environmental conditions such as habitat openness and patch size (Anderson et al. 2019).

In terms of species richness measured in 2019, the median number of native ant species on experimental removal plots was 4 species compared to 6.5 species on control plots with the difference being statistically significant. Given that only two native ant species, on average, were present on experimental plots after treatments concluded, the median number of four species suggests that recovery is underway. Control plots that were invaded prior to the initiation of treatments

experienced a sharp decline in species richness (Naughton et al. 2020). The discrepancy in species richness can also be attributed to the recruitment, growth, and lifespan of the founding colony. Population often is limited by recruitment abilities of a colony, especially the dispersal patterns of the foundress queen (Cole and Wiernasz 2002). Colony size also has an influence on colony growth rate, and a colony of this size may be expected to grow from a few years up to a decade (Shik et al. 2015). Assemblage development also faces further challenges imposed by biotic and abiotic stressors. The species richness levels may also indicate a disconnection between the functional and taxonomic composition of the native ant assemblages due to the fact that functional composition may be more sensitive to environmental changes (Fountain-Jones et al. 2017). The question of whether functional composition should take precedence over taxonomic composition when evaluating community recovery remains to be studied.

Ultimately, the gradual re-assembly of native ants on experimental plots demonstrated the resilience and recovery ability of the ant assemblages to their previous functionalities before invasion, and supports the hypothesis of community recovery after disturbances. The native ant assemblages were able to achieve similar trophic positions as the pre-invaded state, despite the difference in species richness. Future analysis can investigate the correlation between functional and taxonomic composition and evaluate community recovery by weighing the importance of each factor. However, several factors still are at play that may limit or promote the extent to full recovery. This re-colonization is still ongoing and future data collection and analysis will further substantiate the importance of such ecological restoration.

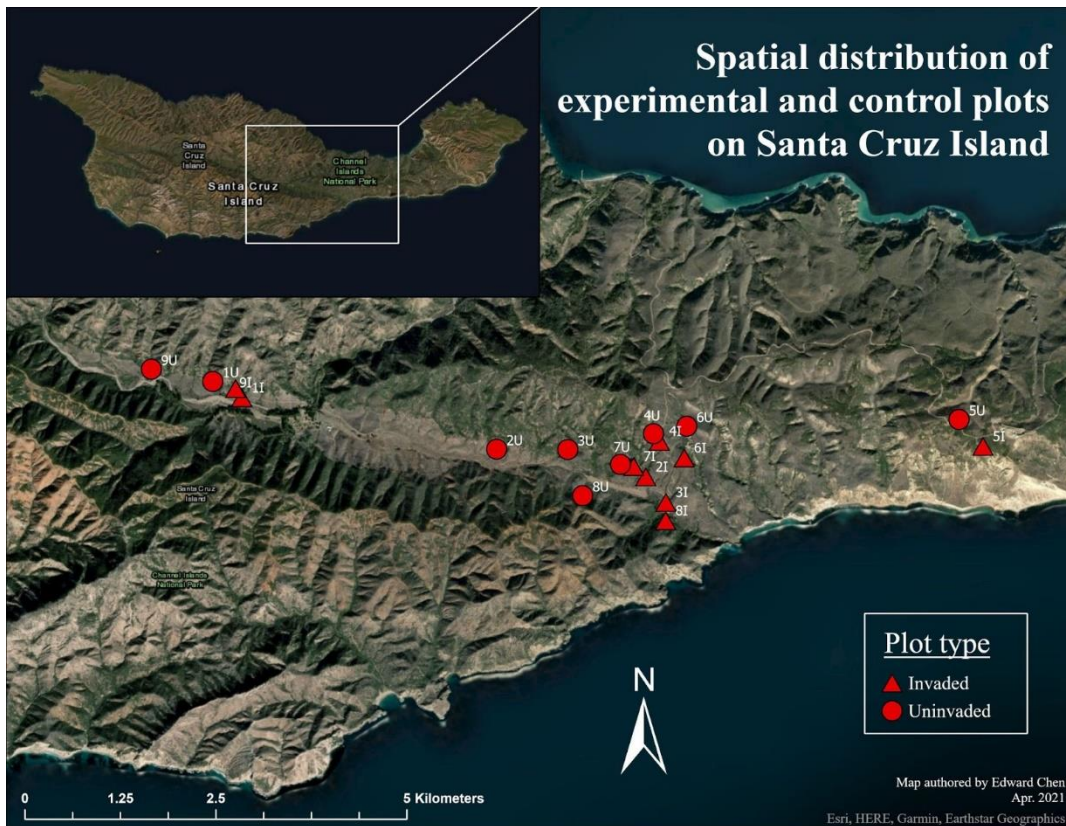


Figure 1 Map of the 18 long-term paired control and experimental plots on Santa Cruz Island.

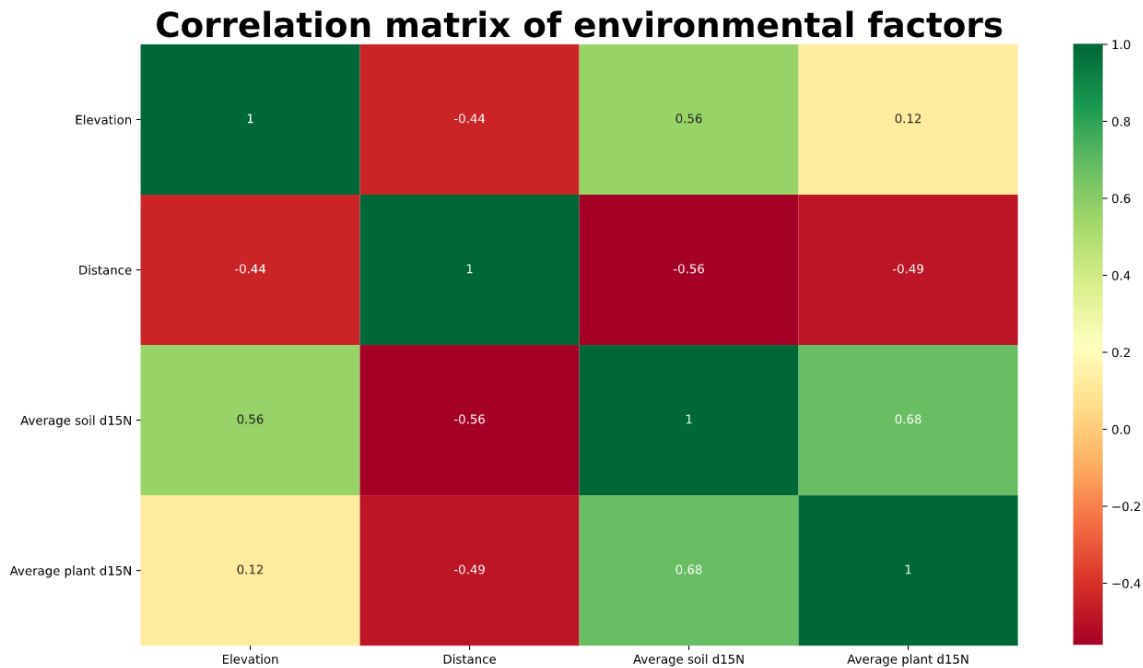


Figure 2 Correlation matrix showing the Pearson's correlation coefficients between each environmental variable.

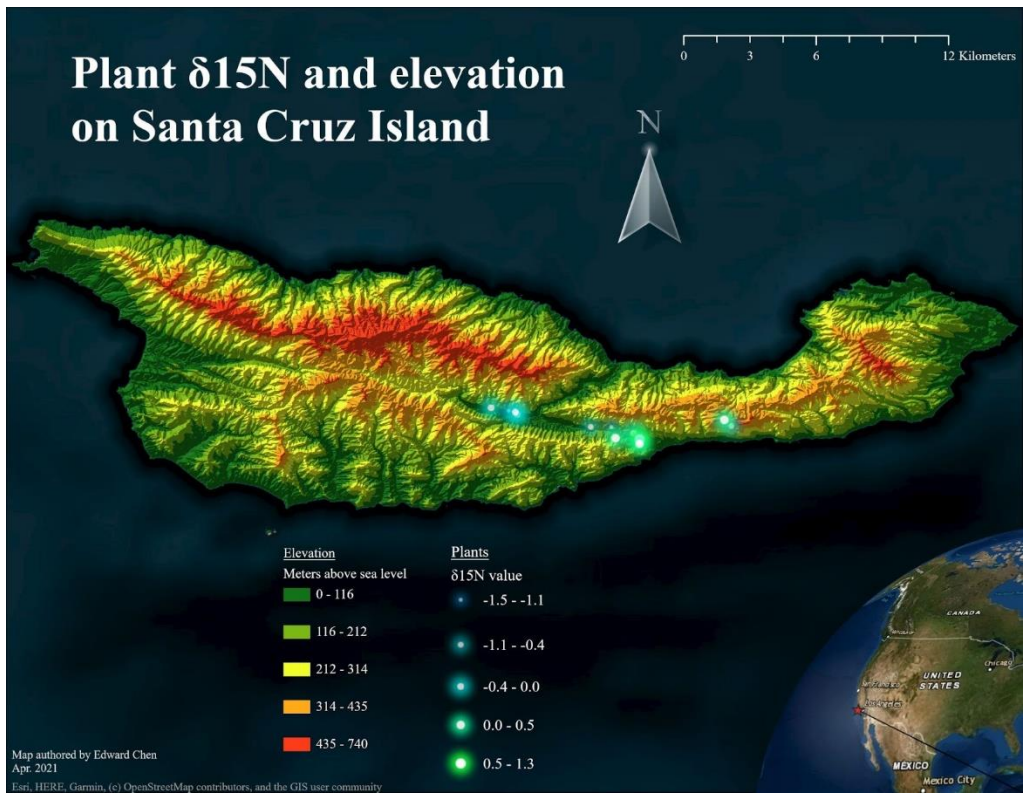


Figure 3 Map of  $\delta^{15}\text{N}$  of plants relative to a Digital Elevation Model on Santa Cruz Island.



Figure 4 Map of  $\delta^{15}\text{N}$  of soil relative to a Digital Elevation Model on Santa Cruz Island.

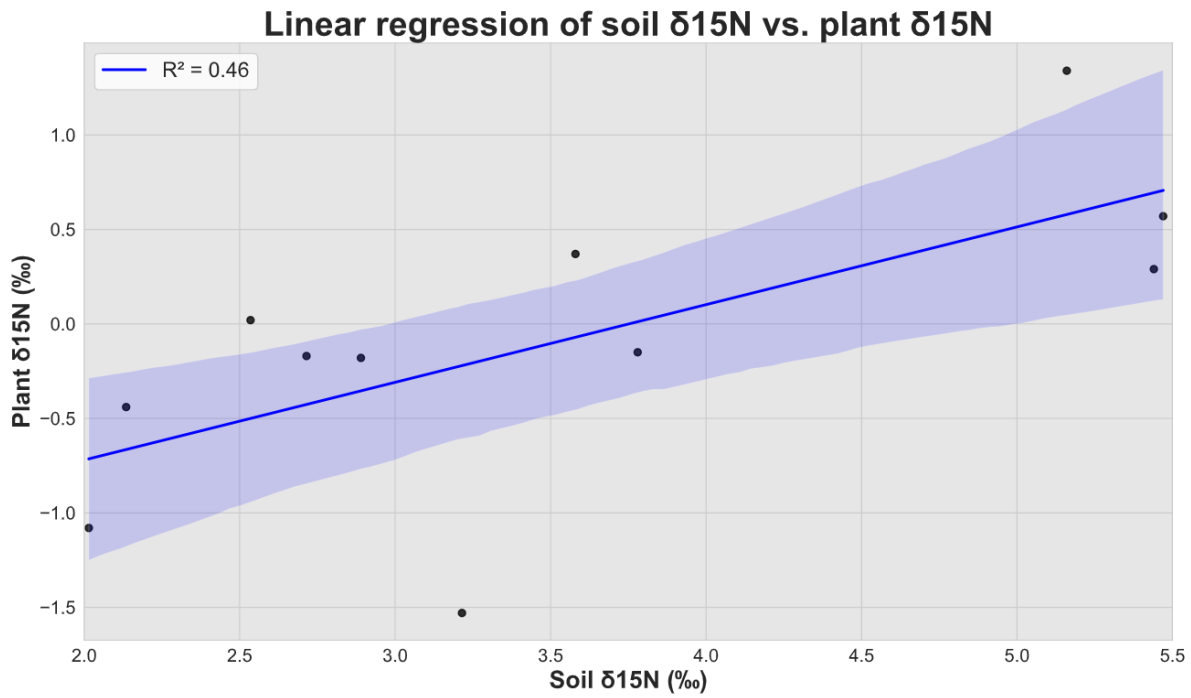


Figure 5 Linear regression of soil  $\delta^{15}\text{N}$  values predicting plant  $\delta^{15}\text{N}$  values. Line shows significant ordinary least squares regression.

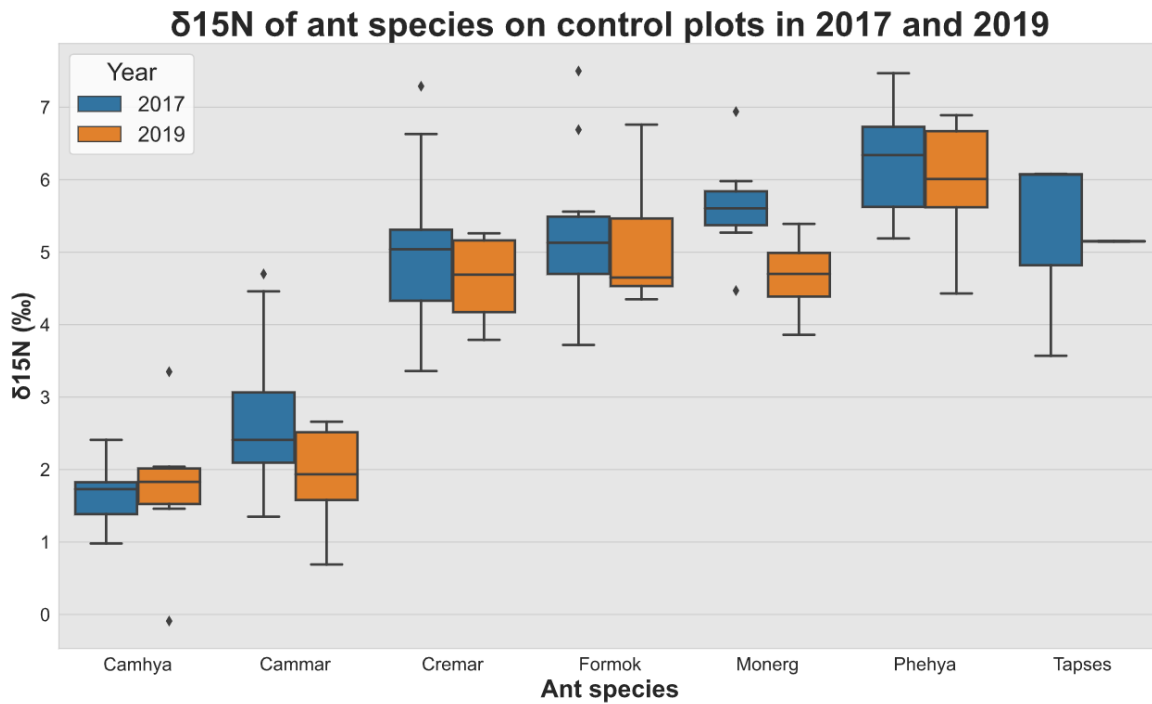


Figure 6  $\delta^{15}\text{N}$  values for seven native ant species on control plots in 2017 and 2019.



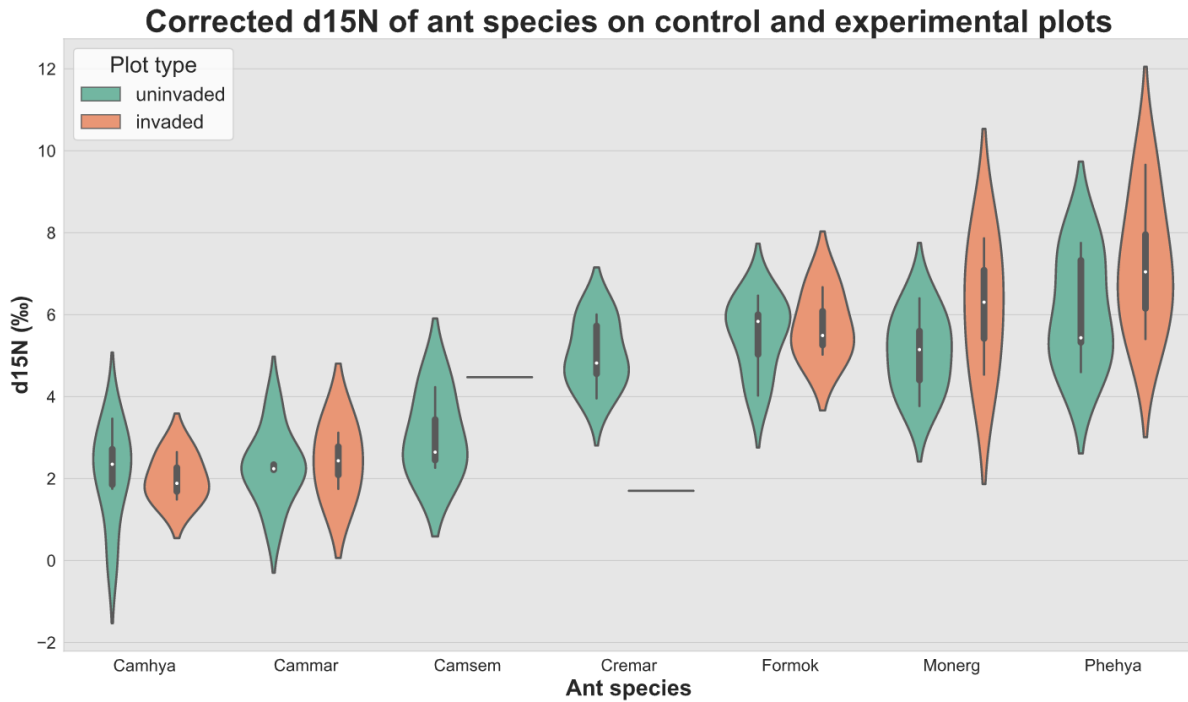


Figure 7 Corrected  $\delta^{15}\text{N}$  values of seven native ant species compared between experimental and control plots.

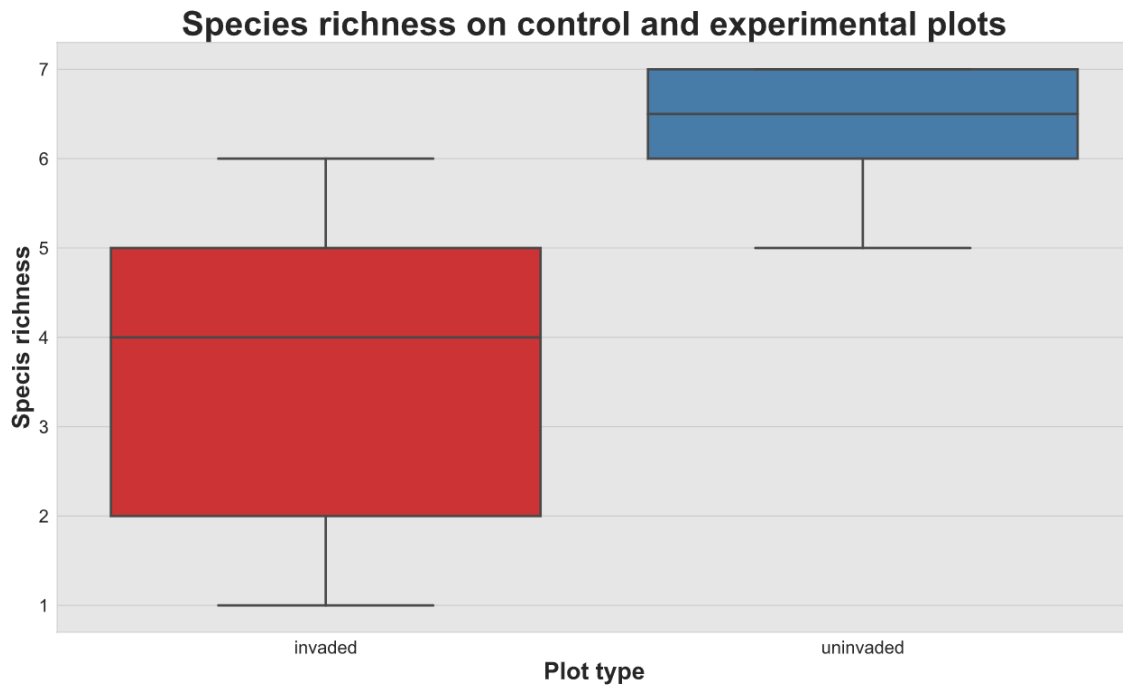


Figure 8 Species richness of native ants on experimental and control plots.

Table 1 List of the twelve species and their aliases identified and sampled from in 2017 and 2019.

<b>Species name</b>	<b>Alias</b>
<i>Camponotus clarithorax</i>	Camcla
<i>Camponotus hyatti</i>	Camhya
<i>Camponotus maritimus</i>	Cammar
<i>Camponotus semitestaceus</i>	Camsem
<i>Creamatogaster marioni</i>	Creemar
<i>Formica moki</i>	Formok
<i>Monomorium ergatogyna</i>	Monerg
<i>Phedole hyatti</i>	Pehya
<i>Polyergus vinosus</i>	Polvin
<i>Prenolepis imparis</i>	Preimp
<i>Solenopsis molesta</i>	Solmol
<i>Tapinoma sessile</i>	Tapses

## APPENDIX

Table A1 Invasion year, GPS coordinates, elevation, distance from shore, sampling year, and treatment year of the 18 long term study plots.

<b>Plot pairs</b>	<b>Year invaded</b>	<b>Latitude</b>	<b>Longitude</b>	<b>Elevation (m)</b>	<b>Distance from shore(m)</b>	<b>Sampling initiated</b>	<b>Years treated</b>
1	<2010	N 33.998372	W 119.724339	77.93427277	3567.021587	2010	2013-2014
1	Never	N 33.999839	W 119.727765	86.64872742	3856.887325	2010	2013-2014
2	<2010	N 33.990634	W 119.676823	121.2479019	1172.866858	2010	2015-2016
2	Never	N 33.993222	W 119.694368	127.8007965	2151.321929	2010	Never
3	<2010	N 33.988138	W 119.674468	100.038002	892.5085845	2010	2015-2016
3	Never	N 33.993177	W 119.685998	158.3710022	1800.692521	2010	Never
4	<2010	N 33.994098	W 119.67522	247.1166992	1375.239963	2010	2015-2016
4	2012	N 33.994735	W 119.675902	258.9361877	1468.556508	2010	2015-2016
5	<2010	N 33.993609	W 119.637166	414.9696045	678.0255518	2010	2013-2014
5	Never	N 33.99611	W 119.639974	433.0451965	956.5052939	2010	Never
6	<2010	N 33.992479	W 119.672307	227.7601929	1089.403258	2011	2015-2016
6	Never	N 33.995469	W 119.672008	261.0817871	1365.730526	2011	2015-2016
7	<2010	N 33.991649	W 119.678255	187.241806	1345.796054	2011	2015-2016
7	2014	N 33.991729	W 119.679799	194.9496002	1404.534446	2011	2015-2016
8	<2010	N 33.986343	W 119.674491	98.76986694	691.8736591	2011	2015-2016
8	Never	N 33.988669	W 119.684259	168.6242981	1275.481316	2011	Never
9	2011	N 33.999256	W 119.725073	96.05653381	3684.945643	2011	2013-2014
9	Never	N 34.001041	W 119.734994	87.96063232	4173.109997	2011	Never

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