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Changes in Argentine ant trophic positions as a function of time since invasion

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

in

Biology

by

Evelyne Baratelli

Committee in charge:

Professor David Holway, Chair
Professor Carolyn Kurle, Co-chair
Professor Jonathan Shurin

2021

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University of California San Diego

2021

DEDICATION

I would like to dedicate this thesis to my parents. I am immensely grateful for their unwavering support and belief in me throughout my undergraduate and graduate degree. This would not have been possible without them.

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ABSTRACT OF THE THESIS

Changes in Argentine ant trophic positions as a function of time since invasion

by

Evelyne Baratelli

Master of Science in Biology

University of California San Diego, 2021

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

The ecological effects of species introductions can change in magnitude over time, but how and why such impacts exhibit temporal variation remains incompletely understood. In this study we used stable isotope analysis to estimate how trophic position changes as a function of the stage of invasion for the Argentine Ant (*Linepithema humile*), a widespread, abundant, and ecologically disruptive invader. Previous studies in southern California found that the trophic position of the Argentine ant was higher at the leading edge of invasion than at sites invaded several years earlier. To assess if a reduction in relative trophic position over time is a common feature of ant invasions, we expanded the temporal and spatial scale of sampling and estimated the relative trophic position of Argentine ants along three invasion chronosequences: Rice Canyon (San Diego Co. CA), the Sacramento River Valley (Yolo and Solano Cos., CA), and San Nicolas Island (Ventura Co., CA).

Resampling Rice Canyon in 2019, 16 years after the original survey, revealed a surprising increase in Argentine ant trophic position. At the two other invasion chronosequences, the trophic position of the Argentine ant did not change with the stage of invasion. These findings suggest that changes in relative trophic position associated with invasion processes may reflect short-term responses, which are not evident in long-term sampling efforts. These findings also point to the potential value of historical data and repeated, annual sampling.

Introduction

The ecological effects of biological invasions can vary with time. Invasions can provoke changes in the invading species, the ecosystems being invaded, and even physical features of the environment (Strayer et al. 2006). For instance, as introduced species establish and spread in new environments, they can undergo changes in their gene expression, resource allocation, morphology, and behavior (Strayer et. al 2006). The short-term and long-term impacts of invasions vary because introduced species can adapt quickly to new habitats (Strayer et. al 2006). However, the changes to the invaded environment can often be slow to emerge, and the long-term impacts are not always immediately apparent (Strayer et. al 2006). For example, a study conducted on the red imported fire ant (*Solenopsis invicta*) revealed that the abundance of this invasive species decreased 12 years after the invasion with concomitant increases in native ant species richness; these patterns provide an example of how the ecological impact of this introduced ant species may be greatest at the beginning of an invasion (Morrison 2002). Long-term invasion impacts are also frequently ecologically damaging. For example, a meta-analysis of invasive terrestrial invertebrates has shown a general decrease in animal abundance and diversity as well as a reduction in the plant fitness of the ecosystems they invade (Cameron et. al 2016).

The Argentine ant (*Linepithema humile*) provides a well-studied example of a widespread and damaging introduced invertebrate species. For instance, the invasion of Argentine ants in the California Channel Islands led to swift decreases in native ant species richness and shifts in species composition (Naughton et. al 2020). The Argentine ant behaves aggressively towards native ant species and is effective at displacing them (Erickson 1971; Holway 1999). In addition to competitive interactions, the Argentine ant limits the establishment of new native ant colonies

by preying upon winged native ant queens (Human & Gordon 1996). The invasive success of this species, as with other invasive ants, can be attributed in part to its ability to form super-colonies (Van Wilgenburg et al. 2010). In addition to displacing native ants, Argentine ants modify species interactions in invaded areas by monopolizing resources and reducing biodiversity. For example, the Argentine ant disrupts plant-animal mutualisms including pollination (Lach 2007) and seed dispersal (Bond and Slingsby 1984). The Argentine ant also limits prey available to insectivores such as the coastal horned lizard and therefore contributes to its population decline in California (Suarez and Case 2002).

Stable isotope analysis can provide insights into the dietary inputs of invasive ants as well as reveal extensive variation in the relative trophic position of individual colonies. Interspecific variation in trophic position is known between native and introduced populations (Tillberg et al. 2007, Wilder et al. 2011, Balzani et al. 2021), as well as spatially and temporally within introduced populations (Tillberg et al. 2007, Menke et al. 2010, Wilder et al. 2011, Roeder and Kaspari 2017, Balzani et al. 2021). For example, both the red imported fire ant and the Argentine ant tend to occupy higher trophic positions (e.g. appear more carnivorous) in their native ranges in Argentina than in their introduced ranges in North America (Tillberg et. al 2007, Wilder et al. 2011). In addition, within introduced populations, the estimated trophic position of individual red imported fire ant colonies varies from that of primary producers to higher order carnivores (Roeder and Kaspari 2017). In general, negative impacts of biological invasions are most common when invasive species are at an equal or higher trophic position than the native species (Bradley et. al 2019).

By following the spread of an expanding Argentine ant invasion front over an eight-year period in southern California, Tillberg et al. (2007) found that the relative trophic position of this

invader was higher at the leading edge of the invasion front than at sites invaded at least one year earlier. Two possible (and non-mutually exclusive) mechanisms might contribute to a reduction in trophic position: (i) prey depletion, and (ii) enhanced availability of plant-based carbohydrate resources, such as honeydew from Hemiptera. Prey depletion could result from the loss of native ants as the invasion proceeds (Menke et al. 2018, Naughton et al. 2020), whereas access to hemipteran honeydew may increase as a function of time since invasion because the Argentine ant effectively tends aggregations of these insects. Diet manipulation studies demonstrate that Argentine ant colonies provided honeydew-producing aphids have lower $\delta^{15}\text{N}$ values than those fed animal-based diets (Menke et. al 2010). In addition, access to honeydew producing aphids increases worker survival, worker activity, and colony growth (Shik et. al 2012).

In this study, we assess the generality of reductions in trophic position as a function of time since invasion. Specifically, we used stable isotope analysis (on nitrogen) to investigate how the relative trophic position of the Argentine ant changes with the stage of invasion at three different locations in California. Stable isotope analysis can offer insights into the diets of omnivores, like the Argentine ant, that consume food in liquid form (Menke et al. 2010). To examine how trophic position changes with respect to the stage of invasion, we resampled the Argentine ant at the previously sampled location in Tillberg et. al (2007) as well as an invasion chronosequence in the Sacramento Valley (Menke et al. 2018), and a series of transects on San Nicolas Island that differed in the position of sampling sites relative to an expanding invasion front. We tested if the Argentine ant exhibits a reduction in trophic position with time since invasion, over greater spatial and temporal scales than before. Clarifying the changing trophic positions of Argentine ants throughout an invasion is critical in determining the impact of this species on the food webs of these California ecosystems.

Methods

We collected Argentine ant samples between late August and late September 2019 at three locations in California: Rice Canyon, Chula Vista, San Diego Co., the lower Sacramento River Valley, Yolo and Solano Cos., and San Nicolas Island, Ventura Co. (Table 1). At Rice Canyon, we collected ants at nine coastal sage scrub sites sampled in previous studies (Suarez et al. 1998, Tillberg et al. 2007, Achury et al. 2021). The nine sites run in a line along the east-west axis of the canyon and are spaced approximately 120 m apart from one another (Tillberg et al. 2007). In the lower Sacramento River Valley, we collected ants at 15 riparian woodland sites that make up an invasion chronosequence used in Menke et al. (2018) to examine the long-term effects of Argentine ant invasions. These sites are evenly distributed among five, widely-spaced blocks; each block includes one site invaded before 1986, one site invaded between 1986 and 1993, and one site invaded between 1993 and 2017 (Menke et al. 2018). On San Nicolas Island, where the Argentine ant has invaded about 20% of the island area (Boser et al. 2018), we collected ants along seven, 200-m transects separated from one another by at least 500 m. Each transect was oriented perpendicular to an invasion front; Argentine ant workers were collected at the invasion front itself and 100 m and 200 m inside the invaded area. This sampling design thus represents a ‘space-for-time’ comparison in which time since invasion presumably increases with distance away from the invasion front along each transect. All collection sites on San Nicolas Island were in open scrub mixed with grassland.

At all three locations 50 to 100 Argentine ant workers were collected by beating perennial vegetation with a beating net. Workers were placed immediately in 95% ethanol and then stored at -20° before processing. At each site, perennial plant material was collected to estimate $\delta^{15}\text{N}$ values for primary producers (as in Gibbs et al. 2014). The plant species collected

differed among the three study locations but were standardized across sites within each location (Table 1). At each site, leaves from three different individuals of each species were collected and placed in paper envelopes. Plants sampled at each site were always within 20 m of where ants were collected. Plant samples were air dried and then stored at -20°.

We processed ant samples by first removing the gaster (all abdominal segments posterior to the petiole) to avoid including what the ants recently consumed. We then placed ants in a drying oven at 55°, homogenized dried material with a clean pestle, and measured 1 mg of homogenized ant tissue from each site into individual tin capsules. For plant samples, we combined an equal mass of dried plant material of each plant species collected at each site and then homogenized this combined material. Homogenized plant material (5 mg representing an even mix of the species collected at each site) was weighed into individual tin capsules. All isotope samples were analyzed at the stable isotope facility at the University of California, Davis using a Europa Hydra 20/20 continuous-flow IRM.

All statistical analyses were performed in R (R Development Core Team 2016). We used a paired *t*-test to determine if $\delta^{15}\text{N}$ values of Argentine ant workers from Rice Canyon changed between 2003 (Tillberg et al. 2007) and 2019 (present study). Given the lack of plant material for the 2003 samples, the comparison involving the Rice Canyon data used $\delta^{15}\text{N}$ values for ants only. Each pair of data, however, represented samples from the same collecting site. For the analysis of the data from the Sacramento River Valley and San Nicolas Island, we used a one-way blocked ANOVA. For these analyses, we subtracted the $\delta^{15}\text{N}$ value of the plant material from each site from the respective $\delta^{15}\text{N}$ value of the ants (as seen in Gibbs et al. 2014). Prior to performing statistical tests, we confirmed that our data met the assumptions of the models used. This exercise revealed the presence of an outlier in the San Nicolas Island data set in which one

of the Argentine ant samples was anomalously low (2.05 compared to 5.37 ± 0.99 (mean \pm SE) for the other sites at the same transect position). Given that there was no replication at the level of individual sites, we excluded the transect (representing three sites) that included this sample from the analysis. Statistical analysis of raw $\delta^{15}\text{N}$ values for plants and ants from the Sacramento River Valley and San Nicolas Island are listed in Table A.1.

Results

The temporal comparison of uncorrected $\delta^{15}\text{N}$ values of Argentine ant workers from Rice Canyon revealed that samples collected in 2019 were higher than those collected in 2003 (Fig. 1; paired t-test: $t = 2.475$, $df = 7$, $P = 0.043$). A closer examination of the Rice Canyon data revealed that the $\delta^{15}\text{N}$ values of Argentine ant workers from individual collecting sites ($n = 8$) were all higher in 2019 than in 2003 with only one exception sampling site (see Fig. 1). The $\delta^{15}\text{N}$ values from 2019 also appear higher than sampling years (2001, 2002 and 2003) from the previous study (Tillberg et. al 2007; Figure A.1). However, this is an imperfect comparison because the Argentine ant was still actively invading the canyon in 2001 and 2002.

Analysis of the Sacramento Valley and San Nicolas Island datasets revealed no pattern of change in $\delta^{15}\text{N}$ values across time. Corrected $\delta^{15}\text{N}$ values of Argentine ant workers from the Sacramento River Valley chronosequences showed no change over time (Fig. 2; one-way blocked ANOVA: $F_{2,4} = 0.324$, $P = 0.732$); there was also no effect of sampling block (Fig. 2; one-way blocked ANOVA: $F_{2,4} = 1.161$, $P = 0.396$). There was also no block effect for the raw ant or plant data from these sites (Table A.1). The San Nicolas Island chronosequence also showed no change in corrected $\delta^{15}\text{N}$ values of Argentine ant workers over time (Fig. 3; one-way blocked ANOVA: $F_{2,6} = 2.716$, $P = 0.106$) or significant block effects (Fig. 3; one-way blocked ANOVA: $F_{2,6} = 1.889$, $P = 0.164$). However, block effects were significant at San Nicolas

Island when $\delta^{15}\text{N}$ values were not corrected using basal plant values (Table A.1). There were also no significant differences in raw ant or plant values between the different time bins (i.e. the points along the transect) at San Nicolas Island or Sacramento Valley. Additionally, the $\delta^{15}\text{N}$ values of plant samples collected at Rice Canyon in 2019 remained uniform across all transects and followed a relatively similar trend to the $\delta^{15}\text{N}$ values of ants (Fig. 4).

Discussion

Invasive ants exhibit considerable spatial and temporal variation in their relative trophic position (Tillberg et al. 2007, Wilder et al. 2011, Roeder and Kaspari 2017, Balzani et al. 2021). We examined if resource assimilation by introduced Argentine ants varied as a function of time since invasion at three locations in California. Resampled sites at Rice Canyon showed a significant increase in the trophic position of ants between 2003 and 2019 (Fig. 1). However, the results from the chronosequences established in the Sacramento River Valley and on San Nicolas Island revealed neither an increase nor a decrease in trophic position over the course of the invasion (Fig. 2-3). These findings suggest that post-invasion reductions in trophic position, as observed in Tillberg et al. (2007), might only be evident soon after invasion or could be evident at some sites but not others.

Results from Rice Canyon allowed us to examine trophic trends for the Argentine ant over a longer time span than that examined in Tillberg et al. (2007). Our results revealed a significantly higher trophic position for the Argentine ant in 2019 than in 2003 (Fig. 1), and this difference could be evidence of a more carnivorous diet in the most recent sampling period. Achury et al. (2021) found that the number of Argentine ant workers captured in pitfall traps in Rice Canyon in 2017 appeared higher than in previous years, and the Argentine ant was also

abundant during the sampling conducted in this study (*personal observation*). It seems plausible that ecosystem-level changes at this site, including increased stormwater runoff and retention, might simultaneously favor Argentine ants, which seem to prefer high soil moisture (Menke et al 2007), and also alter the food resources available to this invader. Freshwater environments, for example, can widely vary in their $\delta^{15}\text{N}$ values because of complex nitrogen cycling processes that lead to isotopic fractionation (Guiry 2019). For instance, the mean $\delta^{15}\text{N}$ of a single salmon species varied by 10‰ between different lakes in North America (Guiry 2019). Increases in environmental $\delta^{15}\text{N}$ values resulting from storm water inputs into Rice Canyon thus seem plausible and would in turn elevate $\delta^{15}\text{N}$ values of resident Argentine ants. These findings suggest that finer scale temporal sampling may be required to clarify long-term changes in the trophic ecology of introduced species.

The chronosequences established at San Nicolas Island and Sacramento Valley provided an opportunity to test the generality of patterns observed at Rice Canyon. Neither site revealed change in $\delta^{15}\text{N}$ as a function of the stage of invasion (Fig. 2 and 3). This lack of change could be a reflection of the long-term outcomes of biological invasions. The most recent invasion time bin at Sacramento Valley ranges from 1994 to 2014 (Fig. 2), and ants at these sites established there at some point since 1994. Therefore, the decrease in trophic position observed Tillberg et al. (2007) may have been transitory and thus not evident in long-term data sets. The temporal scales in the San Nicolas Island data set were likely much shorter (Fig. 3). Research has shown that the rate of spread during an Argentine ant invasion is often 10-20 m/ year (Holway 1998; Boser et al 2018). For this reason, invasions sampled at San Nicolas Island were likely all less than a decade old. Prey depletion could explain the lack of change in trophic position at these shorter time frames. Limited prey availability would result in relatively uniform trophic positions regardless

of the time since invasion. Our results complement previous studies on Argentine ants which have demonstrated their ability to remain highly abundant and negatively impactful for long periods of time (Menke et al. 2018, Achury et al. 2021). This unchanging nature of invasion impacts is not restricted to Argentine ants. For example, a study conducted on introduced peacock bass in Lake Gatun, Panama showed that the invader was still abundant and ecologically damaging 45 years after its introduction (Sharpe et. al 2017). Our results emphasize the importance of evaluating the effects of invasive species over various temporal and spatial scales.

A caveat of our study is the lack of plant data collected from Rice Canyon in 2003, preventing us from calculating a baseline $\delta^{15}\text{N}$ value which would help to eliminate the possibility of environmental factors driving the $\delta^{15}\text{N}$ values of the Argentine ants. The $\delta^{15}\text{N}$ values of plants can reflect the temperature and precipitation of an ecosystem (Amundson et. al 2003) as well as resource availability (Dawson et. al 2002). However, the inclusion of the two other sets of chronosequence data helps mitigate this by providing more evidence that Argentine ant populations do not uniformly decrease in trophic position with time since invasion. Some of the differences in $\delta^{15}\text{N}$ values can be attributed to natural variations from site to site. For example, the average $\delta^{15}\text{N}$ values of the Argentine ants at San Nicolas Island were higher than those from Sacramento Valley (Fig. 2, Fig. 3). The ecosystem at San Nicolas Island likely experiences nutrient inputs from marine sources, which could increase the overall $\delta^{15}\text{N}$ values of organisms there (Anderson et. al 1998; Paetzold et. al 2008). This study was also constrained by the large variation in temporal scales used between the three study locations which limit our ability to make direct comparisons. However, this also lends strength to the study by allowing for long-term assessments of Argentine ant invasions (emphasized in Strayer et. al 2006) and broadening the scope of the initial study (Tillberg et. al 2007).

Our study demonstrates that we cannot assume that the invasive Argentine ant will decrease its trophic position over the course of their invasion in a new range. The pattern observed in Tillberg et al. (2007) may be confined to certain temporal scales. Invasive species often change and acclimatize to their new habitat over short time periods (Strayer et al. 2006). However, Argentine ants are particularly complex because while a lot of invasive species experience rapid evolutionary changes at the beginning of an invasion, these ants hardly change due to their tendency to form super-colonies leaving them in “evolutionary stasis” (Van Wilgenburg et al. 2006). Therefore, exploring the resource assimilation of the Argentine ant over a variety of temporal and spatial scales is essential. As noted above, the ecological impacts of Argentine ant invasions can persist for decades (Menke et al. 2018, Achury et al. 2021). Furthermore, ants are considered to be ecosystem engineers that can affect various organisms and the chemical and physical environment they reside in (Folgarait 1998). Our work further demonstrates the importance of long-term studies for investigating biological invasions. Many outcomes of invasions such as changes to the invaded environment and their overall impact can often be slow and continuous (Strayer et al. 2006) and difficult to adequately detect or describe over shorter time scales. For this reason, short-term studies on invasions may reveal incomplete trends that are part of a larger biological process. Future work on Argentine ant invasions would be strengthened by including a variety of temporal scales and long-term assessments as well as repeated annual sampling.

I would like to thank Dr. David Holway for his advice and contributions to this work. I would also like to thank Dr. Carolyn Kurle, Dr. Jonathan Shurin and Dr. Ida Naughton for their guidance and support.

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REFERENCES

- Achury, R., Holway, D. A., & Suarez, A. V. (2021). Pervasive and persistent effects of ant invasion and fragmentation on native ant assemblages. *Ecology*, *102*(3).
<https://doi.org/10.1002/ecy.3257>
- Amundson, R., Austin, A. T., Schuur, E. A. G., Yoo, K., Matzek, V., Kendall, C., Uebersax, A., Brenner, D., & Baisden, W. T. (2003). Global patterns of the isotopic composition of soil and plant nitrogen. *Global Biogeochemical Cycles*, *17*(1). <https://doi.org/10.1029/2002gb001903>
- Anderson, W. B., & Polis, G. A. (1998). Marine Subsidies of Island Communities in the Gulf of California: Evidence from Stable Carbon and Nitrogen Isotopes. *Oikos*, *81*(1), 75.
<https://doi.org/10.2307/3546469>
- Balzani, P., Vizzini, S., Frizzi, F., Masoni, A., Lessard, J., Bernasconi, C., Francoeur, A., Ibarra-Isassi, J., Brassard, F., Cherix, D., & Santini, G. (2021). Plasticity in the trophic niche of an invasive ant explains establishment success and long-term coexistence. *Oikos*, *130*(5), 691–696.
<https://doi.org/10.1111/oik.08217>
- Boser, C. L., Merrill, K., Fisher, R. N., Naughton, I., & Holway, D. A. (2018). The Introduced Argentine Ant (*Linepithema humile*) on the California Channel Islands: Distribution and Patterns of Spread. *Western North American Naturalist*, *78*(4), 820. <https://doi.org/10.3398/064.078.0421>
- Bond, W., & Slingsby, P. (1984). Collapse of an Ant-Plant Mutualism: The Argentine Ant (*Iridomyrmex humilis*) and Myrmecochorous Proteaceae. *Ecology*, *65*, 1031-1037.
- Bradley, B. A., Laginhas, B. B., Whitlock, R., Allen, J. M., Bates, A. E., Bernatchez, G., Diez, J. M., Early, R., Lenoir, J., Vilà, M., & Sorte, C. J. B. (2019). Disentangling the abundance–impact relationship for invasive species. *Proceedings of the National Academy of Sciences*, *116*(20), 9919–9924. <https://doi.org/10.1073/pnas.1818081116>
- Cameron, E. K., Vilà, M., & Cabeza, M. (2016). Global meta-analysis of the impacts of terrestrial invertebrate invaders on species, communities and ecosystems. *Global Ecology and Biogeography*, *25*(5), 596–606. <https://doi.org/10.1111/geb.12436>

- Dawson, T. E., Mambelli, S., Plamboeck, A. H., Templer, P. H., & Tu, K. P. (2002). Stable Isotopes in Plant Ecology. *Annual Review of Ecology and Systematics*, 33(1), 507–559. <https://doi.org/10.1146/annurev.ecolsys.33.020602.095451>
- Erickson, J. M. (1971). The Displacement of Native Ant Species by the Introduced Argentine Ant *Iridomyrmex humilis* Mayr. *Psyche: A Journal of Entomology*, 78(4), 257–266. <https://doi.org/10.1155/1971/34713>
- Folgarait, P. J. (1998). Ant biodiversity and its relationship to ecosystem functioning: a review. *Biodiversity and Conservation*, 7(9), 1221–1244. <https://doi.org/10.1023/a:1008891901953>
- Gibb, H., Stoklosa, J., Warton, D. I., Brown, A. M., Andrew, N. R., & Cunningham, S. A. (2014). Does morphology predict trophic position and habitat use of ant species and assemblages? *Oecologia*, 177(2), 519–531. <https://doi.org/10.1007/s00442-014-3101-9>
- Guiry, E. (2019). Complexities of Stable Carbon and Nitrogen Isotope Biogeochemistry in Ancient Freshwater Ecosystems: Implications for the Study of Past Subsistence and Environmental Change. *Frontiers in Ecology and Evolution*, 7. <https://doi.org/10.3389/fevo.2019.00313>
- Holway, D. A. (1998). Factors governing rate of invasion: a natural experiment using Argentine ants. *Oecologia*, 115(1–2), 206–212. <https://doi.org/10.1007/s004420050509>
- Holway, D. A. (1999). Competitive Mechanisms Underlying the Displacement of Native Ants by the Invasive Argentine Ant. *Ecology*, 80(1), 238–251.
- Human, K. G., & Gordon, D. M. (1996). Exploitation and interference competition between the invasive Argentine ant, *Linepithema humile*, and native ant species. *Oecologia*, 105(3), 405–412. <https://doi.org/10.1007/bf00328744>
- Lach, L. (2007). Argentine ants displace floral arthropods in a biodiversity hotspot. *Diversity and Distributions*, 14(2), 281–290. <https://doi.org/10.1111/j.1472-4642.2007.00410.x>

Menke, S. B., Fisher, R. N., Jetz, W., & Holway, D. A. (2007). Biotic and abiotic controls of Argentine ant invasion success at local and landscape scales. *Ecology*, 88(12), 3164–3173. <https://doi.org/10.1890/07-0122.1>

Menke, S. B., Suarez, A. V., Tillberg, C. V., Chou, C. T., & Holway, D. A. (2010). Trophic ecology of the invasive Argentine ant: spatio-temporal variation in resource assimilation and isotopic enrichment. *Oecologia*, 164(3), 763–771. <https://doi.org/10.1007/s00442-010-1694-1>

Menke, S. B., Ward, P. S., & Holway, D. A. (2018). Long-term record of Argentine ant invasions reveals enduring ecological impacts. *Ecology*, 99(5), 1194–1202. <https://doi.org/10.1002/ecy.2200>

Morrison, L. W. (2002). Long-term impacts of an arthropod-community invasion by the imported fire ant, *Solenopsis Invicta*, *Ecology*, 83(8), 2337–2345.

Naughton, I., Boser, C., Tsutsui, N. D., & Holway, D. A. (2020). Direct evidence of native ant displacement by the Argentine ant in island ecosystems. *Biological Invasions*, 22(2), 681–691. <https://doi.org/10.1007/s10530-019-02121-7>

Paetzold, A., Lee, M., & Post, D. M. (2008). Marine resource flows to terrestrial arthropod predators on a temperate island: the role of subsidies between systems of similar productivity. *Oecologia*, 157(4), 653–659. <https://doi.org/10.1007/s00442-008-1098-7>

Roeder, Karl & Kaspari, Michael. (2017). From cryptic herbivore to predator: Stable isotopes reveal consistent variability in trophic levels in an ant population. *Ecology*. 98. 297–303. [10.1002/ecy.1641](https://doi.org/10.1002/ecy.1641).

Sharpe, D. M. T., De León, L. F., González, R., & Torchin, M. E. (2017). Tropical fish community does not recover 45 years after predator introduction. *Ecology*, 98(2), 412–424. <https://doi.org/10.1002/ecy.1648>

Shik, J. Z., & Silverman, J. (2012). Towards a nutritional ecology of invasive establishment: aphid mutualists provide better fuel for incipient Argentine ant colonies than insect prey. *Biological Invasions*, 15(4), 829–836. <https://doi.org/10.1007/s10530-012-0330-x>

Strayer, D. L., Eviner, V. T., Jeschke, J. M., & Pace, M. L. (2006). Understanding the long-term effects of species invasions. *Trends in Ecology & Evolution*, *21*(11), 645–651.

<https://doi.org/10.1016/j.tree.2006.07.007>

Suarez, A. V., & Case, T. J. (2002). Bottom-up effects on persistence of a specialist predator: ant invasions and horned lizards. *Ecological Applications*, *12*(1), 291–298.

Tillberg, C. V., Holway, D. A., LeBrun, E. G., & Suarez, A. V. (2007). Trophic ecology of invasive Argentine ants in their native and introduced ranges. *Proceedings of the National Academy of Sciences*, *104*(52), 20856–20861. <https://doi.org/10.1073/pnas.0706903105>

Van Wilgenburg, E., Torres, C. W., & Tsutsui, N. D. (2010). The global expansion of a single ant supercolony. *Evolutionary Applications*, *3*(2), 136-143. <https://doi.org/10.1111/j.1752-4571.2009.00114.x>

Wilder, S. M., Holway, D. A., Suarez, A. V., LeBrun, E. G., & Eubanks, M. D. (2011). Intercontinental differences in resource use reveal the importance of mutualisms in fire ant invasions. *Proceedings of the National Academy of Sciences*, *108*(51), 20639–20644. <https://doi.org/10.1073/pnas.1115263108>

Tables

Table 1 Sampling locations, dates and plant species collected.

Fieldwork locations	Rice Canyon	Sacramento Valley	San Nicolas Island
Dates of sampling	Summer (2003); September 16 - 22 (2019)	August 26 - 31 (2019)	September 9 - 12 (2019)
Number of blocks	1	5	7
Plant species collected	<i>Baccharis sarothroides</i> ; <i>Rhus integrifolia</i>	<i>Populus fremontii</i> ; <i>Salix</i> sp.; <i>Quercus lobata</i>	<i>Baccharis pilularis</i> ; <i>Isocoma menziesii</i>

Figures

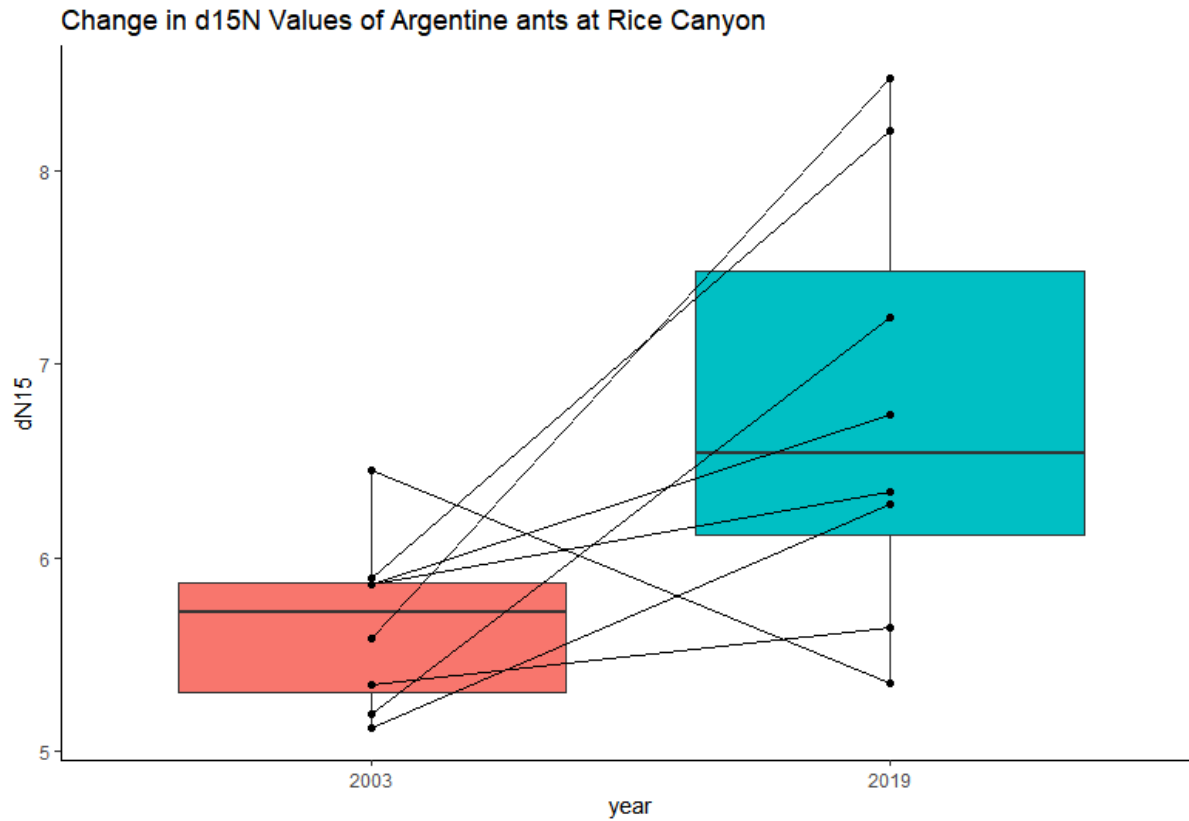


Figure 1 Argentine ant $\delta^{15}\text{N}$ values from Rice Canyon (San Diego Co., CA) in 2003 and 2019. Lines connect $\delta^{15}\text{N}$ values of ants collected at the same sampling station in each of these two years.

Changes in $\delta^{15}\text{N}$ Values of Argentine Ants along a Chronosequence in Sac. Valley

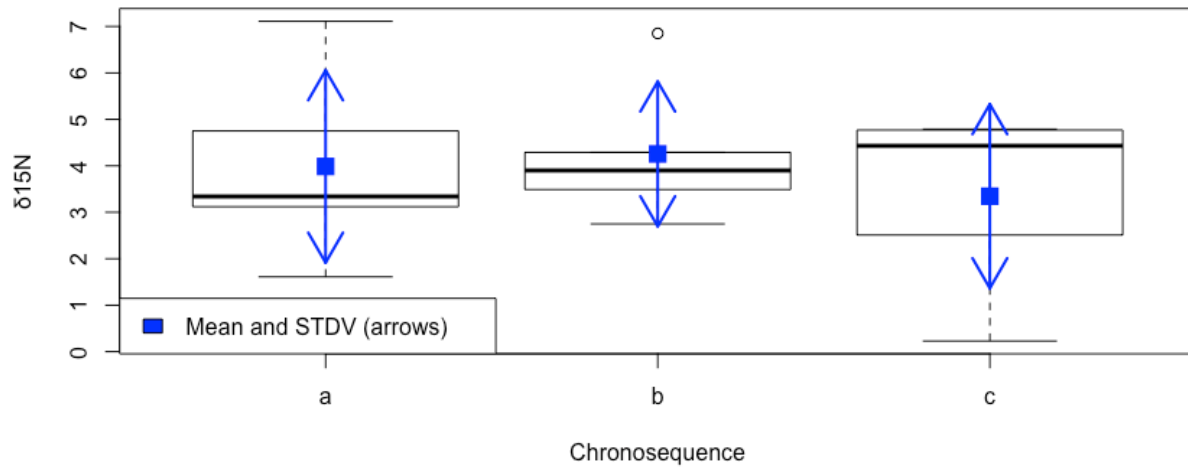


Figure 2 Argentine ant $\delta^{15}\text{N}$ values from an invasion chronosequence in the Sacramento River Valley (Solano and Yolo Cos., CA). 'a' refers to sampling locations invaded by the Argentine ant between 1994 to 2014. 'b' refers to sampling locations invaded by the Argentine ant between 1986 to 1993. 'c' refers to sampling locations invaded by the Argentine ant before 1986.

Change in $\delta^{15}\text{N}$ of Argentine Ants along a Chronosequence at San Nicolas Island

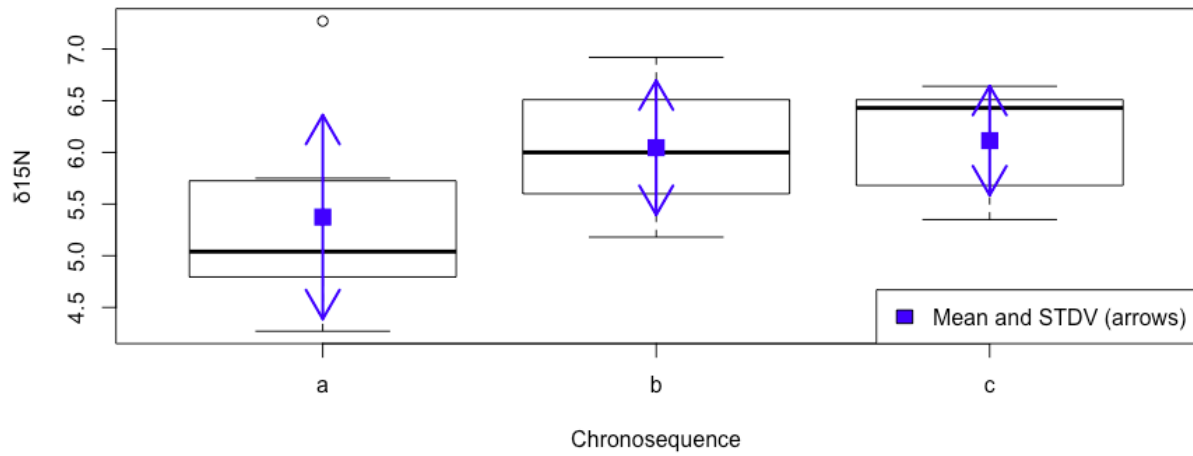


Figure 3 Argentine ant $\delta^{15}\text{N}$ values from transects oriented perpendicular to known contact zones between the Argentine ant and native ants on San Nicolas Island (Ventura Co., CA). ‘a’ refers to sampling locations at the contact zone between the Argentine ant and native ants, ‘b’ refers to sampling locations 100 m inside the contact zone, and ‘c’ refers to sampling locations 200 m inside the contact zone.

Comparison of $\delta^{15}\text{N}$ Values of Plants and Ants from Rice Canyon (2019)

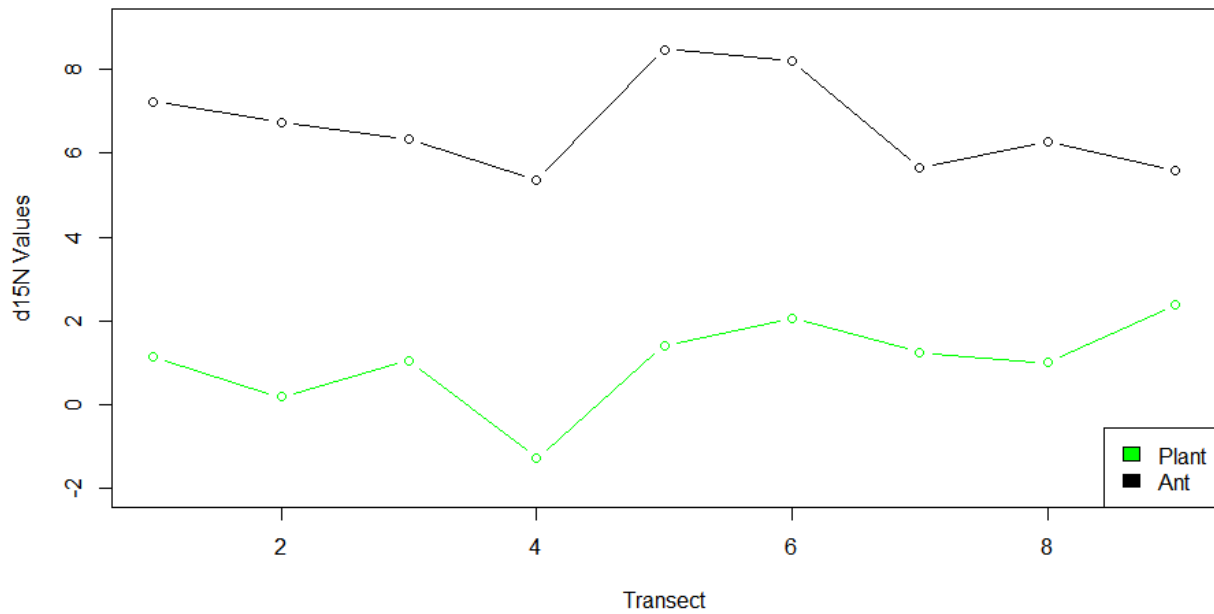


Figure 4 Plant and ant $\delta^{15}\text{N}$ values from Rice Canyon (San Diego Co., CA).

APPENDIX

Table A.1 One-way ANOVA tables of raw ant and plant $\delta^{15}\text{N}$ values from Sacramento Valley and San Nicolas Island.

raw ant $\delta^{15}\text{N}$ values (Sacramento Valley)					
	df	Sum Sq	Mean Sq	F value	Pr(>F)
tm	2	0.976	0.4878	0.972	0.419
blk	4	2.325	0.5814	1.159	0.396
Residuals	8	4.013	0.5017		
raw plant $\delta^{15}\text{N}$ values (Sacramento Valley)					
	df	Sum Sq	Mean Sq	F value	Pr(>F)
tm	2	1.432	0.716	0.257	0.780
blk	4	14.585	3.646	1.308	0.345
Residuals	8	22.295	2.787		
raw ant $\delta^{15}\text{N}$ values (San Nicolas Island)					
	df	Sum Sq	Mean Sq	F value	Pr(>F)
tm	2	0.53	0.265	0.249	0.783383
blk	6	72.39	12.065	11.339	0.000242 ***
Residuals	12	12.77	1.064		
raw plant $\delta^{15}\text{N}$ values (San Nicolas Island)					
	df	Sum Sq	Mean Sq	F value	Pr(>F)
tm	2	3.67	1.833	2.141	0.16024
blk	6	43.94	7.324	8.555	0.00091 ***
Residuals	12	10.27	0.856		

Table A.2 Coordinates of Sampling Locations at San Nicolas Island.

Name	Site	Date	Block	Latitude	Longitude
Niktown	1	Sept 9, 2019	0 m	33.24002	-119.4922
			100 m	33.24099	-119.49179
			200 m	33.24213	-119.49133
	2	Sept 10, 2019	0 m	33.24968	-119.49562
			100 m	33.25051	-119.49577
			200 m	33.25154	-119.49553
	3	Sept 10, 2019	0 m	33.25069	-119.49719
			100 m	33.25131	-119.49643
			200 m	33.25172	-119.49575
	4	Sept 10, 2019	0 m	33.24293	-119.48393
			100 m	33.24375	-119.48304
			200 m	33.24434	-119.48222
Airfield	5	Sept 10, 2019	0 m	33.24365	-119.46169
			100 m	33.24423	-119.46249
			200 m	33.24499	-119.46322
Radar Road	6	Sept 11, 2019	0 m	33.25718	-119.52055
			100 m	33.25621	-119.52015
			200 m	33.25543	-119.52004

Table A.2 Coordinates of Sampling Locations at San Nicolas Island, Continued.

Radar Road	7	Sept 11, 2019	0 m	33.25620	-119.51403
			100 m	33.25559	-119.51354
			200 m	33.25503	-119.51297
	8	Sept 11, 2019	0 m	33.24918	-119.50742
			100 m	33.24900	-119.50812
			200 m	33.24814	-119.50848

Table A.3 Coordinates of Sampling Locations at Rice Canyon.

Site	Latitude	Longitude	Easting	Northing
1	32°38'41.0"N	117°00'54.8"W	32.644714	-117.015223
2	32°38'40.7"N	117°01'01.8"W	32.644633	-117.017168
3	32°38'39.6"N	117°01'09.4"W	32.644329	-117.019286
4	32°38'37.8"N	117°01'16.2"W	32.643837	-117.021168
5	32°38'36.7"N	117°01'23.2"W	32.643531	-117.023103
6	32°38'35.7"N	117°01'31.0"W	32.643257	-117.025273
7	32°38'36.9"N	117°01'39.5"W	32.643591	-117.027648
8	32°38'36.3"N	117°01'46.2"W	32.643426	-117.029493
9	32°38'34.9"N	117°01'53.3"W	32.643023	-117.03146

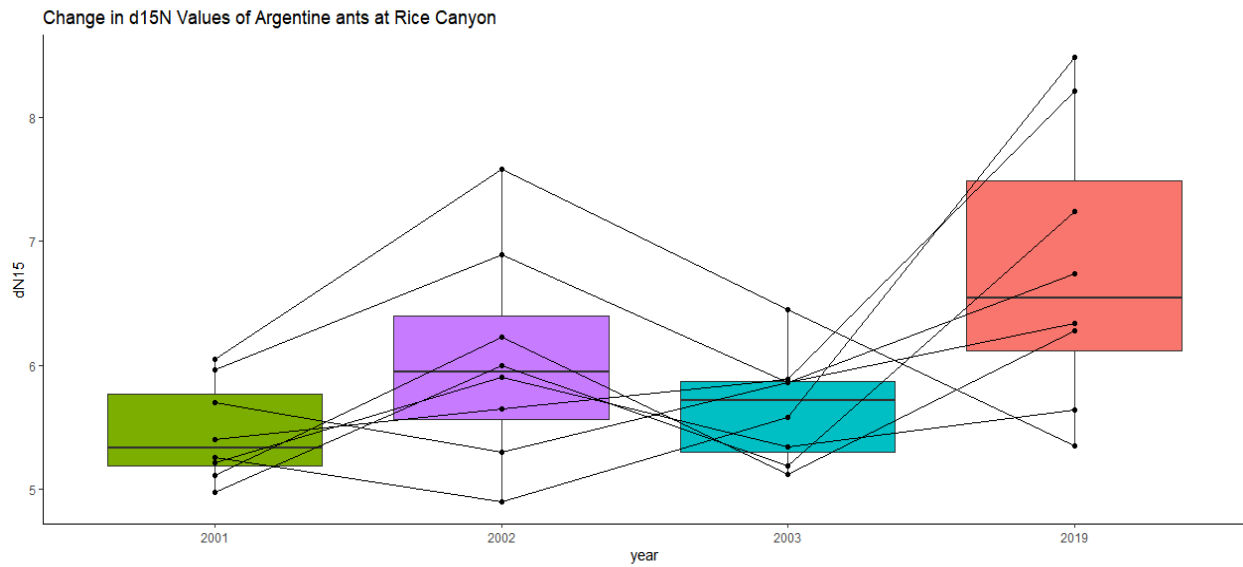
Table A.4 Coordinates of Sampling Locations at Sacramento Valley.

River/Creek	Year Invaded	Block/Site	Latitude	Longitude
Sacramento River P	< 1986	1	38.73841	-121.60396
Sacramento River R	1986-1993	1	38.74952	-121.59707
Sacramento River O	1994-2014	1	38.71831	-121.60783
Sacramento River S	Uninvaded	1	38.7613	-121.5943
Putah Creek 15	< 1986	2	38.50658	-121.98411
Putah Creek 20	1986-1993	2	38.50828	-122.04366
Putah Creek 19	1994-2014	2	38.49646	-122.03595
Putah Creek 21	Uninvaded	2	38.51645	-122.06177
Ulatis Creek R	< 1986	3	38.39916	-122.02885
Ulatis Creek S	1986-1993	3	38.40058	-122.03543
Ulatis Creek T	1994-2014	3	38.40493	-122.04291

Table A.4 Coordinates of Sampling Locations at Sacramento Valley, Continued.

Ulatis Creek U	Uninvaded	3	38.4103	-122.0597
Cache Creek 4	< 1986	4	38.68851	-121.86601
Cache Creek 9	1986-1993	4	38.69077	-121.91853
Cache Creek 8	1994-2014	4	38.68757	-121.90323
Cache Creek 6	Uninvaded	4	38.68285	-121.88921
Cache Creek 14	< 1986	5	38.70985	-122.04774
Cache Creek 10	1986-1993	5	38.69427	-121.93067
Cache Creek 13	1994-2014	5	38.70445	-121.97446
Cache Creek 7	Uninvaded	5	38.68357	-121.89328

Figure A.1 Argentine ant $\delta^{15}\text{N}$ values from Rice Canyon (San Diego Co., CA) sampled in 2001, 2002, 2003, and 2019.



This thesis contains material that is being prepared for submission for publication of the material. Baratelli, Evelyne; Holway, David. The thesis author was a co-author for this material.