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ORIGINAL PAPER

Variation in Argentine ant (*Linepithema humile*) trophic position as a function of time

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Abstract The ecological effects of species introductions can change over time, but an understanding of how and why they do remains hindered by the lack of long-term data sets that permit investigation into underlying causes. We employed stable isotope analysis to estimate how trophic position changes as a function of time for the Argentine ant, a widespread, abundant, and ecologically disruptive introduced species. Previous research at a site in southern California (Rice Canyon, San Diego Co.) found that Argentine ant $\delta^{15}N$ values were higher at the leading edge of invasion than at those same sites in years subsequent to invasion (i.e., after the invasion front had advanced). To assess if a reduction in relative trophic position over time is a typical feature of Argentine ant invasions, we expanded the temporal and spatial scale of sampling and measured $\delta^{15}N$ values of the Argentine ant at three locations with a known or inferred history of invasion: Rice Canyon (the location of the original study), 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 significant increase in Argentine ant $\delta^{15}N$ values. At the two other locations, Argentine ant $\delta^{15}N$ values were independent of time since invasion (Sacramento River Valley) or position relative to the invasion front (San Nicolas Island). These findings suggest that post-invasion reductions in trophic position may not be a general phenomenon or could reflect transitory ecological processes that require finer-scale temporal sampling than was possible to achieve in the present study. Our findings are nonetheless consistent with the results of recent studies, which found that the effects of Argentine ant invasions persist over decadal time scales.

Keywords Invasion · *Linepithema humile* · Stable isotope analysis · Trophic interaction

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Introduction

The ecological effects of biological invasions can change over time. Understanding the basis of such variation requires long-term data sets and quantitative information about the form and magnitude of trophic interactions between an invader and the species with which it interacts (Strayer et al. 2006; Strayer 2012). Temporal variation in resource availability, nutritional demands, and the strength of biotic interactions, for example, may all influence how the trophic position of invaders changes over time. Isolating the underlying causes of this type of variation can reveal insights into evolutionary responses of both the invader and the native species with which it interacts (Strayer 2012). A scarcity of long-term data sets limits an understanding of why invasion impacts vary with time (Simberloff and Gibbons 2004; Strayer et al. 2006).

Introduced ants represent a highly disruptive force in ecosystems worldwide because of their abundance and generalist diet (Holway et al. 2002, Lach and Hooper-Bui 2010). A recent global meta-analysis of invasive terrestrial invertebrates, for example, found that ant invasions were associated with reduced animal abundance and diversity (Cameron et al. 2016). While the ecological effects of ant invasions can persist over decadal time scales (Menke et al. 2018; Achury et al. 2021), some populations of introduced ants have declined in abundance with concomitant reductions in invasion impacts (Lester and Gruber 2016). Progress towards identifying the causes of such declines hinges on understanding how introduced ants interact with other species, especially those that they consume. However, quantifying the diet and trophic position of introduced ant species is complicated by the fact that they are omnivores that feed extensively on liquid foods ranging from honeydew to hemolymph (Tennant & Porter 1991; Holway et al. 2002) and that they also extensively scavenge (Holway & Cameron 2021).

Stable isotope analysis can provide insights into the diets of introduced ants and how resource assimilation varies across space. For example, comparisons of native and introduced populations can suggest causes of niche expansion in the introduced range (Tillberg et al. 2007; Wilder et al. 2011; Suehiro et al. 2017); introduced populations of the red imported fire ant (*Solenopsis invicta*) appear less carnivorous compared to native populations, presumably because of relaxed interspecific competition for carbohydrate resources in their introduced range (Wilder et al. 2011). Introduced ant populations also exhibit spatial variation in estimated trophic position at a variety of scales (Menke et al. 2010; Wilder et al. 2011; Balzani et al. 2021), including among colonies from the same location. Roeder and Kaspari (2017), for example, found that the estimated trophic position of individual red imported fire ant colonies varies from primary consumer to carnivore even within a single population in Oklahoma.

Temporal variation in the estimated trophic position of introduced ants has received less attention compared to spatial variation. Temporal comparisons are important, however, given that (i) invasion impacts can change as a function of time since establishment (Strayer et al. 2006; Strayer 2012), and (ii) introduced ant populations can decrease in abundance over time (Lester and Gruber 2016). By following the spread of an expanding Argentine ant invasion front over an eight-year period at a site (Rice Canyon) in southern California, Tillberg et al. (2007) found that the $\delta^{15}N$ values for this invader were higher at the leading edge of invasion than at those same sites in the years subsequent to invasion. Two possible (and non-mutually exclusive) mechanisms might explain this pattern: (i) prey depletion, and (ii) enhanced availability of carbohydrate resources, such as honeydew from Hemiptera. Prey depletion could result from the elimination of native ants (that succumb to the Argentine ant from both competition and predation) as the invasion proceeds (Naughton et al. 2020), whereas access to hemipteran honeydew could increase if densities of honeydew-producing insects themselves increase as a result of being tended by the Argentine ant. Diet manipulation studies demonstrate that Argentine ant colonies provided honeydew-producing aphids have lower $\delta^{15}N$ values than those fed animal-based diets (Menke et al. 2010) as well as increased worker survival, worker activity, and colony growth (Shik and Silverman 2012).

Here, we assess the generality of post-invasion reductions in trophic position for the Argentine ant (*Linepithema humile*). Specifically, we used stable isotope analysis to investigate how the relative trophic position of the Argentine ant changes with time since invasion at three different locations in California: the Rice Canyon transect previously sampled in

Tillberg et al. (2007), an invasion chronosequence in the Sacramento Valley (Menke et al. 2018), and replicate transects on San Nicolas Island that were each oriented perpendicular to expanding invasion fronts (Boser et al. 2018). By increasing the spatial and temporal sampling considered by Tillberg et al. (2007), our main objective is to test whether or not ant invasions typically exhibit reductions in trophic position in the years subsequent to invasion.

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; Appendix 1). This time of the year corresponds to the annual peak in Argentine ant worker abundance (Markin 1970) and also the end of the summer dry season in California. Sampling sites at each location were in the same habitat, and perennial vegetation at all sites at all locations was mostly to entirely native.

Details regarding the sampling at each location are as follows. 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). These sites are spaced approximately 120 m apart from one another and collectively form an east–west transect oriented parallel to the drainage (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; Naughton et al. 2020), we collected ants along eight, 200-m transects separated from one another by at least 500 m. Each transect was oriented perpendicular to an invasion front (as in Holway 1998a); Argentine ant workers were collected at the invasion front itself and also at sites 100 m and 200 m inside the invaded area. The sampling scheme on San Nicolas Island thus represents a ‘space-for-time’ comparison in which time since invasion presumably increases with distance away from the invasion front along each transect. Although we don’t know the rate of Argentine ant spread on San Nicolas Island, rates of spread on San Clemente Island and Santa Cruz Island range from 10 to 57 m yr (Boser et al. 2018). These rates are comparable to rates measured elsewhere in California (Holway 1998a). All collection sites on San Nicolas Island were in open scrub mixed with grassland.

At each site at all three locations, 50 to 100 Argentine ant workers were collected off of perennial vegetation with a beating net. Workers were placed immediately in 95% ethanol and then stored at − 20° C before processing. At each site, perennial plant material was also collected to estimate δ^{15}N values for primary producers and to account for site-level variation in δ^{15}N values at each location (Roeder and Kaspari 2017). The plant species collected differed among the three study locations, but plant species were standardized across sites within each location (Table 1). At each site, leaves from three different individuals of each plant species were collected and placed in paper envelopes. Plants sampled at each site were always within 20 m of where ants were collected. After collection plant samples were air dried and then stored at − 20° C.

We processed ant samples by first removing the gaster (all abdominal segments posterior to the petiole) to avoid including what the ants recently consumed in processed material (Tillberg et al. 2006).

Table 1 Sampling locations, dates of sampling, number of statistical blocks (and total number of sites), and plant species collected at each study location. Coordinates for sites at each location are listed in Appendix 1

Location	Sampling dates	Blocks (sites)	Plant species collected
Rice Canyon	16–22 Sep 2019	1 (9)	*Baccharis sarothroides; Rhus integrifolia*
Sacramento Valley	26–31 Aug 2019	5 (15)	*Populus fremontii; Quercus lobata; Salix* sp.
San Nicolas Island	9–12 Sep 2019	7 (21)	*Baccharis pilularis; Isocoma menziesii*

We then placed ants in a drying oven at 55 °C, 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 material. Homogenized plant material (c. 5 mg) 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 version 1.4.1103 (R Core Team 2016). We used a paired *t*-test to determine if δ^{15}N values of Argentine ant workers from Rice Canyon changed between 2003 (Tillberg et al. 2007) and 2019 (present study). In the 2003 data set, δ^{15}N values for the Argentine ant were available from 8 of the 9 transect sites. Given that samples from 2003 did not include plant material; the statistical comparison involving the Rice Canyon data was based on δ^{15}N values (for both 2003 and 2019) for Argentine ant samples. Spatial variation in δ^{15}N values will contribute to the variation in our data set as a whole, but each pair of data in this analysis, however, represented two samples collected from the same transect position at different points in time.

For data collected from the other two locations, we used a one-way blocked ANOVA to compare δ^{15}N values across the invasion chronosequence (Sacramento River Valley as in Menke et al. 2018) or as a function of distance away from the invasion front (San Nicolas Island). Transects are considered spatial blocks in the analysis of the data from San Nicolas Island. To obtain baseline corrected δ^{15}N values, we subtracted the δ^{15}N value of the plant material from each site from the respective δ^{15}N value of the ants. Although baseline corrections have limitations (Kjeldgaard et al. 2021), δ^{15}N plant values are based on samples replicated within and among species (Table 1) to ensure representative estimates of δ^{15}N plant values for each site. Prior to performing statistical tests, we confirmed that our data met the assumptions of the models used. This exercise revealed the presence of an anomalously low outlier in the San Nicolas Island data set; one of the Argentine ant samples ($\delta^{15}\mathrm{N} = 2.05$) from a contact zone site was lower than that of other sites at the same transect position ($\delta^{15}\mathrm{N} = 5.37 \pm 0.99$ (mean ± SE)). Given that there was no replication at the level of individual sites within each transect, we excluded the transect that included this sample from the analysis. Statistical analyses based on raw δ^{15}N values for plants and ants from the Sacramento River Valley and San Nicolas Island are listed in Appendix 2.

Results

The temporal comparison of uncorrected δ^{15}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: $t = 2.48$, df = 7, $P = 0.043$). Moreover, ants collected from the same sampling locations along the Rice Canyon transect individually had higher δ^{15}N values in 2019 than in 2003 except for one site (Fig. 1). δ^{15}N values for plants were not available from the 2003 sampling effort, but the δ^{15}N values for plants (1.022 ± 0.36; mean ± SE) and ants (6.65 ± 0.38) as well as their average difference (5.63; Fig. 2) measured in 2019 broadly overlap measurements of δ^{15}N of plants and the Argentine ant from other locations in southern California (Menke et al. 2010; Tillberg et al. 2007; Hanna et al. 2017).

Analysis of the Sacramento Valley and San Nicolas Island datasets revealed no pattern of change in corrected δ^{15}N ant values as a function of time (Figs. 3–4). Corrected δ^{15}N values of Argentine ant workers from the Sacramento River Valley did not vary across the chronosequence (Fig. 3; one-way blocked ANOVA: $F_{2,4} = 0.32$, $P = 0.73$) or among sampling blocks (Fig. 3; one-way blocked ANOVA: $F_{2,4} = 1.16$, $P = 0.40$). There was also no block or time effect for the plant δ^{15}N values or uncorrected ant δ^{15}N values from these sites (Appendix 2). Corrected δ^{15}N values of Argentine ant workers from San Nicolas Island also showed no change across transect positions (Fig. 4; one-way blocked ANOVA: $F_{2,6} = 2.72$, $P = 0.11$) or among sampling blocks (Fig. 4; one-way blocked ANOVA: $F_{2,6} = 1.89$, $P = 0.16$). However, the block effect was significant for comparisons based on plant δ^{15}N values and uncorrected ant δ^{15}N values in the San Nicolas Island analyses (Appendix 2). The effect of time since invasion, however, was not significant in either of these latter analyses (Appendix 2).

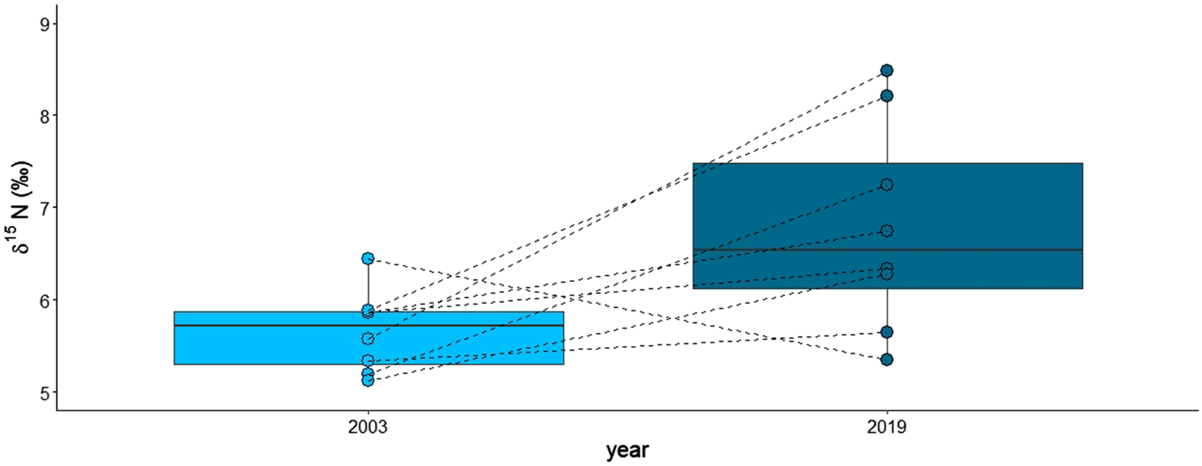

Fig. 1 Argentine ant δ^{15}N values from Rice Canyon (San Diego Co., CA) in 2003 and 2019. Lines connect δ^{15}N values of ants collected at the same transect position in each of these two years

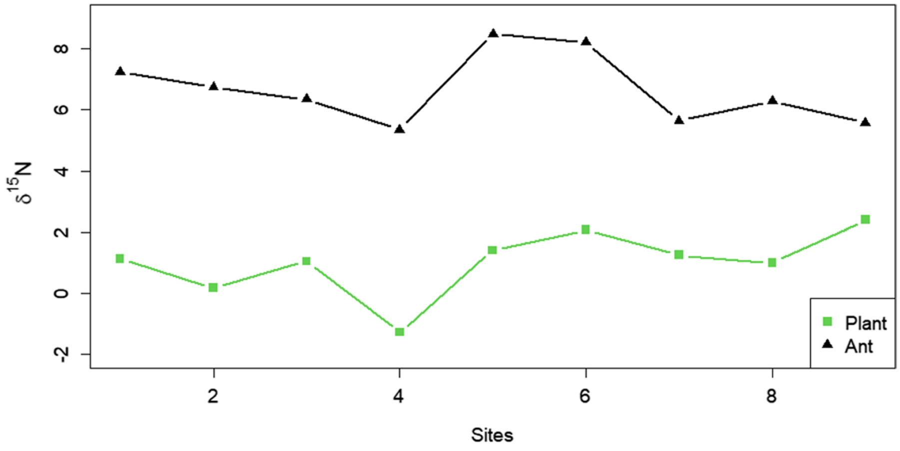

Fig. 2 Plant and ant δ^{15}N values from samples collected in 2019 from Rice Canyon (San Diego Co., CA). Note that there is no replication at the level of transect position for plant and ant δ^{15}N values

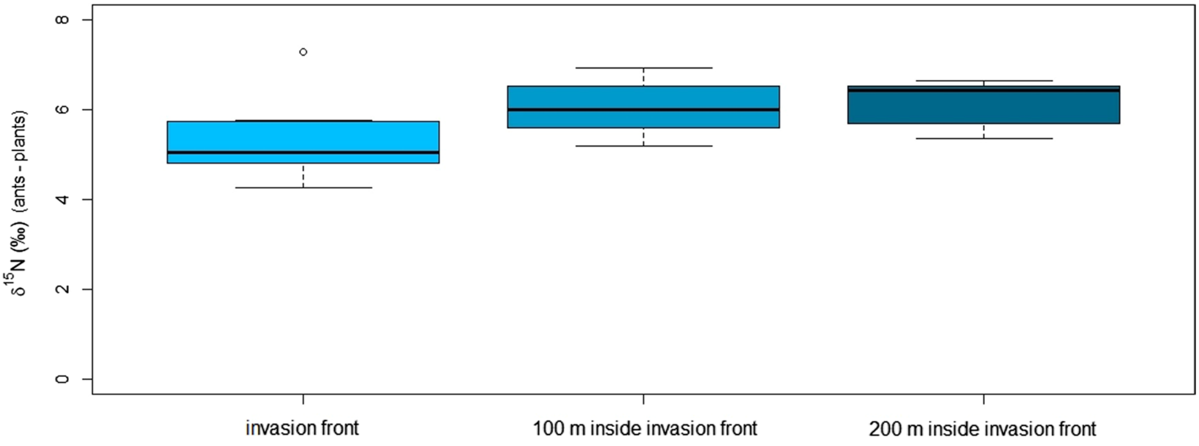

Fig. 3 Argentine ant δ^{15}N values from an invasion chronosequence in the Sacramento River Valley (Solano and Yolo Cos., CA)

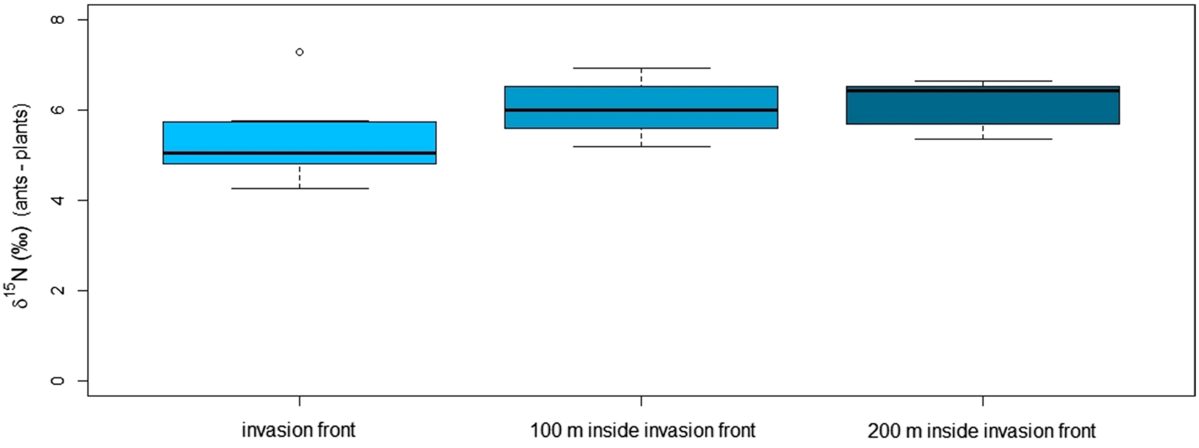

Fig. 4 Argentine ant δ^{15}N values from transects oriented perpendicular to known contact zones between the Argentine ant and native ants on San Nicolas Island (Ventura Co., CA)

Discussion

We expanded the temporal and spatial scale of previous sampling efforts to assess how the trophic ecology of ant invasions changes as a function of time since invasion. At three different locations in California, Argentine ant δ^{15}N values either increased (one location) or did not change (two locations) as a function of time. These findings suggest that post-invasion reductions in trophic position, as observed in Tillberg et al. (2007), could be evident at some sites but not others or that they reflect transitory ecological processes that require finer-scale temporal sampling than that possible to achieve in the present study.

A resurvey of Rice Canyon allowed us to examine changes in Argentine ant δ^{15}N values over a longer time span than that examined in Tillberg et al. (2007). The significant increase in Argentine ant δ^{15}N values between 2003 and 2019 (Fig. 1) could reflect greater assimilation of food resources from high trophic levels than in the original survey, but identifying the basis of this difference would require additional information about the food web at this location and how the location itself might have changed over the past 16 years. Increased urbanization in the areas surrounding Rice Canyon over the past two decades seems likely to have benefitted the Argentine ant. In particular, increased run off resulting from urban irrigation could have elevated Argentine ant abundance (Menke et al. 2007). In support of this hypothesis, Achury et al. (2021), who employed sampling that closely emulated that used in Tillberg et al. 2007, found that the number of Argentine ant workers captured in pitfall traps in Rice Canyon in 2017 appeared higher than in the early 2000s. Increased worker abundance, associated with increased irrigation, might permit the Argentine ant to access resources unavailable to it when present at lower densities. Although native ants at this site mostly disappeared soon after invasion (Suarez et al. 1998; Tillberg et al. 2007) and have largely remained absent (Achury et al. 2021), elevated soil moisture from urban runoff could have altered this site in ways that affected the Argentine ant's trophic ecology. Lastly, differences in the sampling approaches (pitfall traps (Tillberg et al. 2007) *versus* branch beating (present study)) and the time of year of sampling (June 2003 (Tillberg et al. 2007) *versus* September 2019 (present study)) might have also affected our estimates of Argentine ant δ^{15}N.

Analysis of Argentine ant δ^{15}N values from San Nicolas Island and Sacramento Valley also yielded no evidence of post-invasion reductions in relative trophic position. Unlike the areas surrounding Rice Canyon, the sampling sites on San Nicolas Island and in the Sacramento Valley have not been subject to urbanization. Our finding that Argentine ant δ^{15}N values were independent of time since invasion complements the findings of Menke et al. (2018) and Achury et al. (2021); both studies found that Argentine ant presence is associated with sustained reductions in native ant diversity and abundance over decadal time scales. There is growing evidence from a variety of introduced animal taxa that invasion impacts can be chronic and evident over long time scales (Sharpe et al. 2017; Doody et al. 2017).

Although none of the analyses performed in this study supported the existence of post-invasion reductions in relative trophic position, finer-scale (i.e., at least annual) temporal sampling (as performed in Tillberg et al. 2007; Menke et al. 2010; Roeder and Kaspari 2017) might be necessary to detect this type of change. It is noteworthy that we found twice as much variation in δ^{15}N values among sample sites at Rice Canyon in 2019 compared to 2003. Such variation could reflect spatial variation in resource availability (e.g., Roeder and Kaspari 2017; Hanna et al. 2017). Given that native ant displacement by the Argentine ant occurs within a year of invasion (e.g., at Rice Canyon (Tillberg et al. 2007) and on the Channel Islands (Naughton et al. 2020)), annual sampling would be required to detect a post-invasion drop in trophic position if this shift primarily results from prey depletion caused by the elimination of native ants (e.g., Tillberg et al. 2007). The loss of native ants would seem to be the most likely form of prey depletion at these sites given that comparisons of non-ant arthropod richness and abundance from the lower Sacramento Valley (Holway 1998b) and the Channel Islands (Hanna et al. 2015) have revealed no differences between sites with and without the Argentine ant.

Progress towards understanding how the ecological effects of invasions change over time will typically require quantitative information about the diets of introduced species. Stable isotope analysis can provide useful information about the relative importance of plant-based versus animal-based dietary inputs. However, the diets of introduced ants are diverse and encompass living prey, carrion, and liquid exudates from plants and honeydew producing insects. The results of stable isotope analysis can be misinterpreted when the trophic positions of known herbivores and predators are compared to those of ant species that act in part as predators but that also assimilate carrion from animals that occupied multiple trophic levels (Holway & Cameron 2021). Caution thus seems warranted in the interpretation of spatial and temporal comparisons of invasion impacts based solely on stable isotope data.

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Data availability The datasets generated in this study have been uploaded to Dryad (https://doi.org/10.5061/dryad.pc866t1rv).

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