Trophic ecology of invasive Argentine ants in their native and introduced ranges

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Although the ecological effects of invasions often become obvious soon after introduced species become established, more gradual effects may take years to manifest and can thus require long-term data for quantification. We analyzed an 8-year record of stable isotope data on Argentine ants (*Linepithema humile*) from southern California to infer how the trophic position of this widespread invasive species changes over time as native ant species are displaced. We couple this longitudinal analysis with a biregional comparison of stable isotope data (δ^{15}N) on ants from Argentina (native range) and California (introduced range) to quantify (*i*) how the trophic position of *L. humile* differs between native and introduced populations, and (*ii*) how relative trophic position as estimated by δ^{15}N values of Argentine ants compare with those of other ants at the same site. Both long-term and biregional comparisons indicate that the Argentine ant's relative trophic position is reduced at sites with a longer history of occupation. Over the course of 8 years, the relative trophic position of *L. humile* remained high at the leading edge of an invasion front but declined, on average, behind the front as native ants disappeared. Relative to native populations, where *L. humile* is among the most carnivorous of ants, Argentine ants from California occupied lower trophic positions. These results support the hypothesis that Argentine ants shift their diet after establishment as a result of resource depletion and increasing reliance on plant-based resources, especially honeydew-producing Hemiptera. Our results demonstrate the value of long-term and biregional data in uncovering ecological effects of invasions.

biological invasions | stable isotopes | food webs

Biological invasions threaten biodiversity and drain economic resources. Despite the importance of species introductions, the short-term and small-scale nature of most invasive species research is a recognized limitation of this field (1). Additionally, confounding environmental factors can obscure links between the spread of invasive species and decline of natives (2). Spatiotemporal fluctuations in the population sizes of introduced species (3) that result from changes in resource use or availability (4) can greatly alter the extent to which invaders disrupt ecosystems. Because a better understanding of such variation will inform both ecological theory and management strategies, there is an urgent need for long-term studies as well as for research that investigates ecological interactions in the native ranges of introduced species.

One underappreciated source of variation regarding introduced species concerns dietary flexibility and shifts in trophic position between native and introduced populations. This form of ecological plasticity may enhance invasion success in a number of ways. Species capable of extracting required nutrients from multiple trophic levels might establish in a broader range of environments compared with more specialized consumers. Furthermore, theory predicts diminishing biomass at higher trophic levels, suggesting that species feeding at lower trophic levels might attain greater abundance (5).

In this study we examine the direct effects of Argentine ant (*Linepithema humile*) invasions on native ant diversity and then quantify how dietary flexibility in this widespread invader affects spatiotemporal variation in its trophic position. Invasive ants provide an ideal system to test how trophic flexibility contributes to invasion success. With many species introductions, it can be difficult to separate the effects of the invader from covarying factors, such as habitat disturbance, that might also negatively affect natives (2, 6). Because Argentine ants aggressively displace above-ground foraging native ants (7), changes in the diet of *L. humile* that occur during and just after invasion can be linked to native ant displacement. Second, invasive ants, such as *L. humile*, are highly omnivorous and frequently form nonspecialized associations with honeydew-producing Hemiptera (7–10). Greater use of honeydew and other plant-based resources in introduced populations might result in a decrease in trophic position (relative to that of native populations), such that invasive ants would persist at higher densities than if they were acting as carnivores (7, 11, 12). Similar arguments have been proposed to explain the great abundance of ants in tropical rainforest canopies (13). Although the exploitation of honeydew and other plant-based resources might subsidize invasive ants at high densities, few data are available to evaluate this hypothesis.

An important obstacle in this area of research concerns the quantification of ant diets. Incomplete dietary information greatly hinders an understanding of the community-wide effects of ant invasions. Invasive ants forage extensively on liquids (11, 14, 15), so observational data on diets are of limited use, because the exact composition of consumed or stored liquids remains unknown (e.g., the relative proportions of nectar, honeydew, and hemolymph). For these reasons, we use stable isotope analysis, an approach of demonstrated value in quantifying trophic relationships in ants (13, 16, 17).

We combine longitudinal and biregional comparisons (*i*) to track changes in nitrogen isotopic ratios of Argentine ants over time (i.e., as they actively displace native ants), and (*ii*) to compare the trophic position of *L. humile* between its native and introduced ranges. To measure changes in Argentine ant trophic position and native ant diversity during the course of an invasion, we sampled an active invasion front over an 8-year period. We predict that the trophic level of resources assimilated by *L. humile* will drop if the process of invasion either (*i*) depletes resources from high trophic levels (e.g., the consumption of
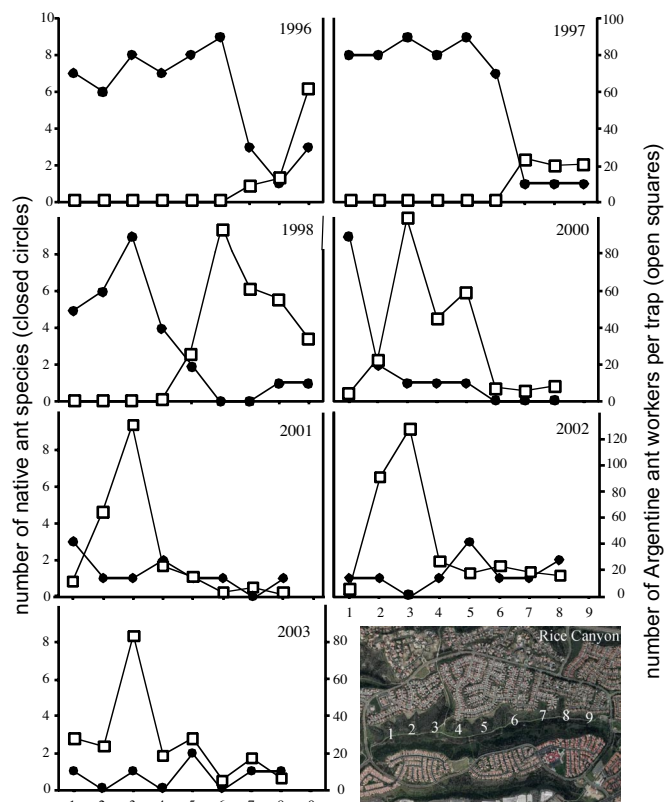

Fig. 1. Displacement of native ants by Argentine ants over an 8-year period in Rice Canyon, San Diego County, California. Sampling stations (1–9) are shown on the x axis. Open squares, number of Argentine ant workers captured per pitfall trap at each sampling station; closed circles, number of native ant species captured in pitfall traps at each sampling station. The photograph (*Bottom Right*) shows an aerial view of Rice Canyon (coastal sage scrub surrounded by residential development) and the approximate location of the center of each sampling station. Image provided by Google Earth.

native ants and other arthropod predators), or (*ii*) leads to increased exploitation of plant-based resources. Alternatively, a downward shift in trophic position would not be expected if resources exploited by Argentine ants remained stable through time, or if plant-based resources, such as honeydew, were lacking. We also perform a biregional comparison of *L. humile* trophic position between multiple native and introduced populations to test whether *L. humile* shifts its trophic position between Argentina and California. These comparisons also yield a wealth of information about the ant communities and the arthropod food webs in both ranges.

Results

Temporal Shifts in Trophic Position. Annual sampling of the Rice Canyon invasion front revealed the steady westward expansion of Argentine ants from the eastern end of the canyon starting in 1996 (Fig. 1). Each year after 1996, *L. humile* occurred at sampling stations progressively farther west until 2001, when it reached the western end of the canyon. The number of *L. humile* workers captured in pitfall traps each year reached its maximum at sampling stations just behind the invasion front (Fig. 1). Argentine ants displaced native ants as soon as they entered Rice Canyon (Fig. 1). Over the 8-year period of sampling, for example, 7.5 ± 0.4 native ant species were captured at sampling stations without Argentine ants (i.e., before invasion), whereas only 1.1 ± 0.1 species were captured at stations with Argentine ants (i.e., after invasion). In

Table 1. Native ant species detected in Rice Canyon, San Diego County, California

Genus and species	Before invasion (1996)	After invasion (2003)
Dorymyrmex bicolor	X	
Dorymyrmex insanus	X	
Tapinoma sessile	X	
Forelius mccooki	X	
Brachymyrmex depilis	X	
Paratrechina cf. *terricola*	X	
Camponotus fragilis	X	
Camponotus yogi	X	
Prenolepis imparis	X	
Stenamma diecki	X	
Pheidole hyatti	X	
Pheidole vistana	X	
Pheidole clementensis	X	
Crematogaster mormonum	X	
Crematogaster californica	X	
Solenopsis xyloni	X	
Solenopsis molesta	X	X
Temnothorax andrei	X	X
Messor andrei	X	
Cyphomyrmex wheeleri	X	
Neivamyrmex californicus	X	
Neivamyrmex nigrescens	X	
Pseudomyrmex apache	X	

Rice Canyon as a whole, the number of native ant species dropped from 23 before 1996 to just 2 by 2003 (Table 1).

As *L. humile* spread through Rice Canyon and displaced resident ants (Fig. 1), its average $\delta^{15}N$ value decreased over the 8-year period of investigation (Fig. 2A). For seven of the nine fixed sampling stations, the $\delta^{15}N$ value for the first year that *L. humile* was recorded at a station (i.e., at the leading edge of the invasion front) exceeded that of the mean $\delta^{15}N$ value for that station in all subsequent years (i.e., after the displacement of native ants) (paired *t* test: $t_8 = 3.07$, $P = 0.0154$) (Fig. 2B).

Biregional Comparisons of Trophic Ecology. At our six study sites in Argentina and California, $\delta^{15}N$ values for ants as a whole encompassed a broad range of values (Fig. 3), suggesting that ants at each site occupy several trophic levels. Minimum to maximum spans of $\delta^{15}N$ are as follows: 7.8‰ at Herradura, 6.4‰ at Ocampo, 5.9‰ at Otamendi, 3.7‰ at Sweetwater, 5‰ at Elliot, and 7.3‰ at Torrey Pines. These ecosystems (especially those in Argentina) include several ant species with $\delta^{15}N$ values overlapping those of herbivores and many ant species with $\delta^{15}N$ values similar to or higher than those of predacious, non-ant arthropods (Fig. 3).

At all native range sites, *L. humile* had $\delta^{15}N$ values equal to or higher than those of syntopic predatory arthropods, whereas at all introduced range sites, *L. humile* had $\delta^{15}N$ values equal to or lower than those of syntopic predatory arthropods (Fig. 3). Moreover, Argentine ants from California had a lower trophic position compared with those from Argentina (nested ANOVA: $F_{1,46} = 14.01$, $P < 0.001$) (Fig. 4). Significant differences in $\delta^{15}N$ also exist among sites ($F_{4,46} = 3.38$, $P < 0.05$). Tukey comparisons indicate that the trophic position of Argentine ants at Torrey Pines is lower than that of *L. humile* from both Herradura and Otamendi, and that the trophic position of Argentine ants from Elliot is lower than that of *L. humile* from Herradura. In addition to ant diversities that were two to three times higher than those of California sites, Argentina sites included a preponderance of ant species with $\delta^{15}N$ values similar to or higher
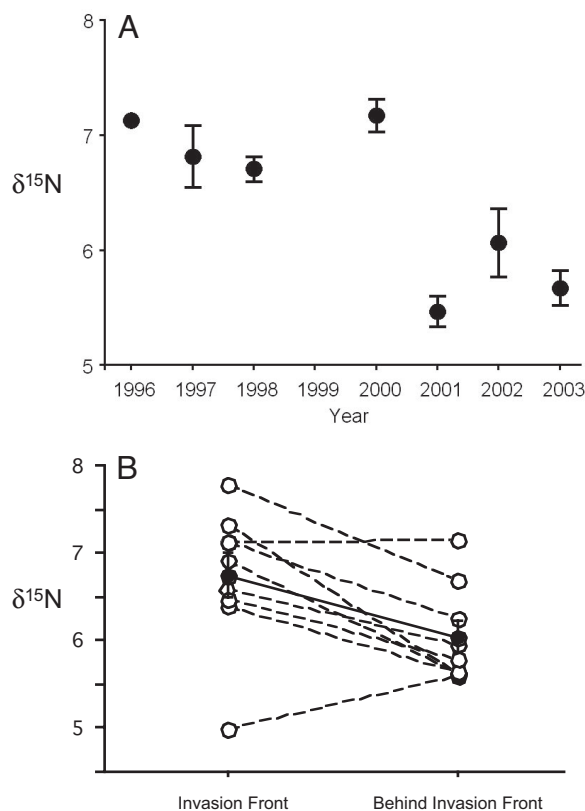
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Fig. 2. Trophic ecology of Argentine ants at an active invasion front. (*A*) Mean (±SE) $\delta^{15}N$ values for Argentine ants invading Rice Canyon from 1996 to 2003. For each year, $\delta^{15}N$ values are averaged over sampling stations at which Argentine ants were present. (*B*) For each of the nine sampling stations in Rice Canyon, the $\delta^{15}N$ value for the first year that *L. humile* was recorded at a sampling station (i.e., at the leading edge of the invasion front) vs. the mean $\delta^{15}N$ value for that station in all subsequent years (i.e., after the displacement of native ants). The solid line and closed circles represent the mean (±SE) values across all sample stations.

than those of predacious, non-ant arthropods. At Herradura, the genus *Ectatomma* and the army ants *Neivamyrmex* and *Labidus* had the highest $\delta^{15}N$ values; these patterns are consistent with the known predatory behavior of these genera. Many ant species at Ocampo also had $\delta^{15}N$ values overlapping those of predacious non-ant arthropods, with a few genera (*Forelius, Pheidole, Odontomachus,* and *Pogonomyrmex*) having $\delta^{15}N$ values 1.5–3 ‰ higher than the mean $\delta^{15}N$ for non-ant predators. Although *Odontomachus* is highly predatory, *Forelius* and *Pheidole* probably obtain protein through both predation and scavenging. *Pogonomyrmex*, although typically a seed-harvesting genus, also collects insect prey (18). The species at Ocampo had a $\delta^{15}N$ of 9.1 ‰, which is 3.3 ‰ higher than the $\delta^{15}N$ of a homogenized sample of their seeds (5.8 ‰). This suggests that a high value of $\delta^{15}N$ may not always result from a predatory diet and reinforces the importance of direct observations and natural history information in trophic ecology research.

Within native range sites, the relative ranking of $\delta^{15}N$ values of Argentine ants vs. those of other ants appears influenced by the number of predatory ant species present. At Herradura and Ocampo, for example, the mean $\delta^{15}N$ for *L. humile* ranks near the middle of the $\delta^{15}N$ values of other ants, with genera such as *Neivamyrmex, Ectatomma,* and *Labidus* ranking higher than *L. humile* (Fig. 3 *a* and *b*). At Otamendi, a more southerly site and one where *L. humile* had a relatively high mean $\delta^{15}N$ value (Fig. 3*c*), ants in several key predacious genera (e.g., *Labidus, Odon-*

tomachus) do not occur (with the exception of *Neivamyrmex*, which we did not find) (19).

At the other end of the spectrum, native range sites (especially Herradura and Ocampo) also include numerous ant species with $\delta^{15}N$ values similar to those of syntopic herbivorous insects. Examples of such ants include twig and tree nesting *Cephalotes, Crematogaster, Camponotus, Myrmelachista,* and *Pseudomyrmex*. Although some of these genera also occur at our California sites, Herradura and Ocampo included numerous taxa strongly to wholly associated with perennial vegetation. Such behavior is nearly absent among ants at our California sites (the only exceptions being *Liometopum occidentale* and *Pseudomyrmex apache*).

Discussion

An understanding of the community-wide effects of invasions requires detailed information about trophic ecology. We use longitudinal and biregional comparisons (*i*) to track changes in the trophic position of Argentine ant invasions over time and (*ii*) to compare ant communities in multiple food webs in Argentina and California. At an active invasion front in southern California, we found that the relative trophic position of *L. humile* declines over time simultaneously with the displacement of native ants. Moreover, introduced populations of *L. humile* have a lower trophic position, on average, compared with native populations. These results support the hypotheses that dietary flexibility and reduction in trophic level can contribute to invasion success.

By measuring annual changes in the number of native ant species during the invasion of Rice Canyon, we obtained a chronological record of native ant displacement. Sampling stations ahead of the invasion front always captured 6–10 native ant species, but as Argentine ants moved progressively through the canyon, native ants declined sharply right at the invasion front and remained low thereafter (Fig. 1). As Argentine ants advanced, the only native ants that remained were *Temnothorax andrei* and *Solenopsis molesta* (Table 1), two small hypogeic species that appear resilient to *L. humile* (2, 20, 21).

Argentine ants peaked in local abundance at sampling stations just behind the leading edge of the invasion front (Fig. 1). This pattern, an initial wave of high density followed by lower numbers of individuals through time, is a common feature of invasions (3) and may result from a reduction in resources exploited by the invader. This may also be a consequence of the unicolonial colony structure typical of introduced populations of this species (22); Argentine ants can redistribute workers and nests closer to areas where resources (23) or competitive interactions are highest. Even though the density of *L. humile* declined over time, native ant diversity failed to rebound during the course of the study. As predicted, the trophic position of *L. humile* at the leading edge of the invasion front exceeded that behind the front (Fig. 2). During the course of the invasion, ants at the front of the invasion presumably displaced native ants through a combination of competition and predation (18, 24, 25). Observations of *L. humile* raiding the nests of native ant species such as *Pogonomyrmex subnitidus, Messor andrei,* and *Solenopsis xyloni* support the contention that native ants may be eliminated by consumption (18). Behind the front, however, with almost no native ants to compete with or to consume, Argentine ants appeared to acquire N from lower trophic levels. Interannual differences in mean $\delta^{15}N$ values (Fig. 2*B*) may have also reflect prevailing environmental conditions. The sampling period included winters that were abnormally wet (1997–1998) and dry (2001–2002), which may have influenced the availability of resources such as arthropod prey.

The biregional comparison of the Argentine ant's trophic position further supports the proposition that dietary flexibility and exploitation of plant-based resources could contribute to invasion success. As a whole, the omnivorous ant community in Argentina
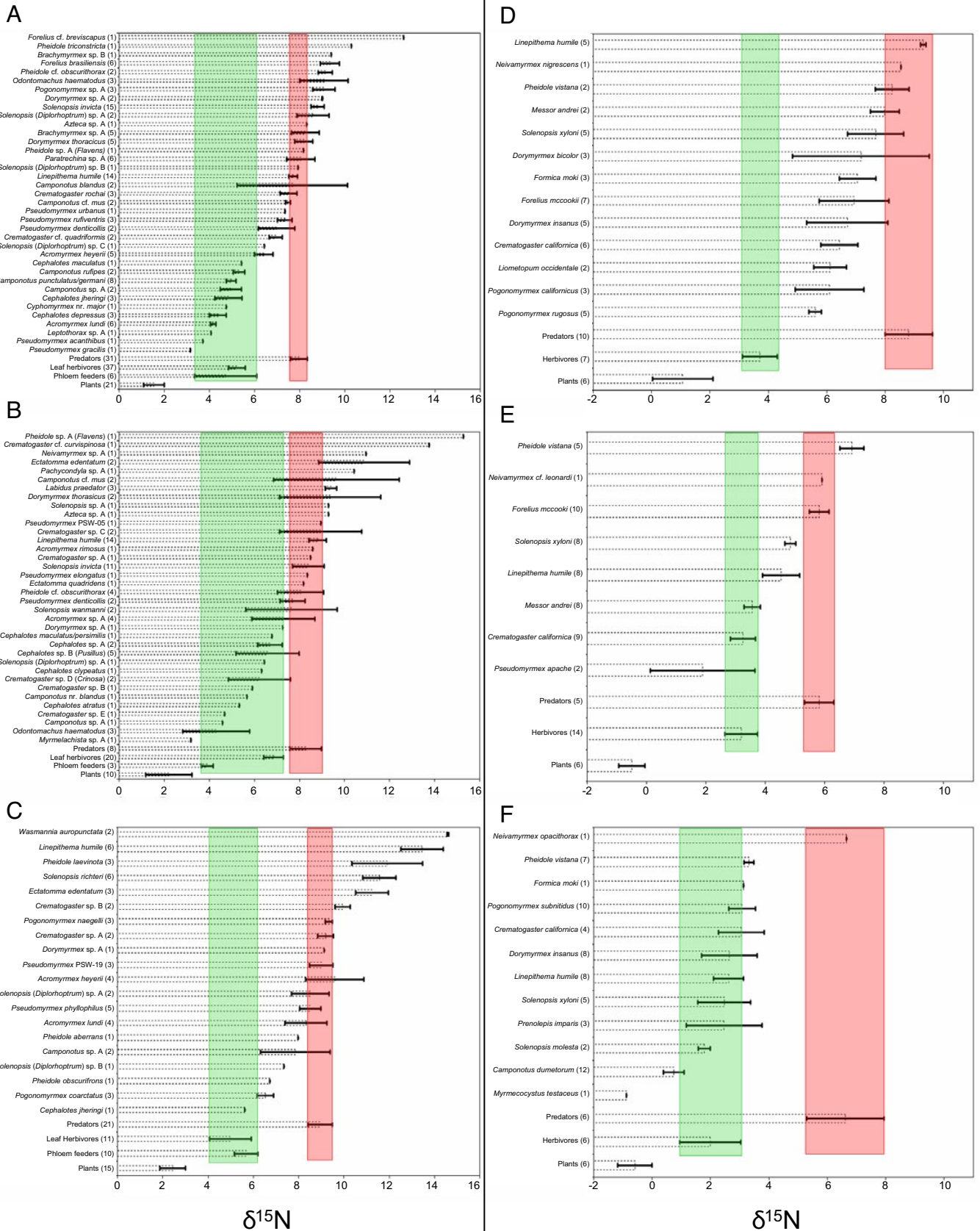
Fig. 3. Mean (±SE) δ^{15}N values of ants, plants, and herbivorous and predacious arthropods at three native range sites in Argentina [(A) Ocampo, (B) Herradura, and (C) Otamendi)] and three introduced range sites in California [(D) Sweetwater, (E) Elliot, and (F) Torrey Pines]. Numbers in parentheses indicate the number of replicates (colonies) for each species. Names in parentheses indicate species groups. Shading indicates δ^{15}N values of herbivorous (green, left vertical bars) and predacious (red, right vertical bars) arthropods at each site.

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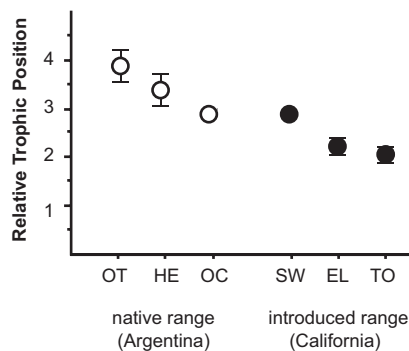
Fig. 4. Mean (±SE) relative trophic position of Argentine ants from three native range sites in Argentina [Ocampo (OC), Herradura (HE), and Otamendi (OT)] and three introduced range sites in California [Torrey Pines (TP), Elliot (EL), and Sweetwater (SW)]. The number of Argentine ant nests sampled at each location is reported in Fig. 3.

exhibits a more enriched nitrogen signature compared with that of the Californian ant community. This disparity may reflect the greater availability of arthropod carrion in the more productive Argentine subtropics (26). The Argentine ant's ability to achieve high densities in the relatively less-productive scrub environments of California is a testament to its dietary flexibility and perhaps a consequence of the loss of native ants with which *L. humile* competes. Relative to introduced populations, native populations of *L. humile* occupy a higher trophic position (Fig. 4) and appear to obtain much of their N from animal-based resources. Although several ant genera exceed *L. humile* in their δ^{15}N values, the mean δ^{15}N values for Argentine ants overlapped the range of δ^{15}N values for predacious non-ant arthropods (Fig. 3). This pattern suggests that the primary input of N into Argentine ant colonies is protein from predation and scavenging, rather than from plant-based N from nectar or hemipteran honeydew.

Compared with the findings of Davidson *et al.* (13) for tropical rainforest canopy ants, the ants of floodplain woodlands in Argentina span a similar range of δ^{15}N values and include many presumed omnivores (Fig. 3). However, the ground-foraging ant communities from Argentina are skewed toward animal-based N (Fig. 3), whereas many canopy ants appear to obtain N predominantly from plant-based sources (13). This disparity points to key differences between the competitive environments of epigeic ants in subtropical woodlands and arboreal ants in tropical rainforests (see also ref. 27). The extensive overlap in δ^{15}N values between *L. humile* and other ants suggests that competition for animal-based protein is fierce, a contention supported by LeBrun *et al.* (28).

This study found support for two mechanisms that favor invasion success: (*i*) flexible patterns of resource use and (*ii*) a shift to a lower trophic position in new environments. The proximate causes of these dietary changes are unclear. In California, honeydew-producing insects may be more abundant (e.g., in citrus agroecosystems) or more accessible as a result of depauperate arboreal ant faunas (Fig. 3). Alternatively, a drop in trophic position might result from the depletion of high-trophic level resources from invaded areas. Although arthropod surveys from California show that many predacious arthropods (especially spiders and carabid beetles) remain abundant in areas invaded by Argentine ants (29–31), dramatic declines in native ant abundance might represent the depletion of an important high-trophic-level resource. Future work that focuses on teasing apart these alternative, but not mutually exclusive, hypotheses for the pattern reported here may provide insight into the mechanisms behind shifts in trophic position in this species.

Materials and Methods

Stable Isotope Analysis. Stable isotope analysis measures the relative abundance of naturally occurring, stable (i.e., nonradioactive) forms of biologically relevant elements, such as nitrogen (N). This method allows the tracking of nutrients and energy through food webs and can thus clarify trophic relationships that are otherwise difficult to quantify (32–35). A general result of isotope studies is that consumers are usually enriched relative to their prey (i.e., predators have a higher ^{15}N/^{14}N ratio). Studies on insects generally report a δ^{15}N enrichment of 2–3‰ per trophic level (16, 36–40), although this value can vary depending on the organism, its age, or the quality of the food resource (40–42).

Temporal Shifts in Trophic Position. To determine whether the δ^{15}N values of *L. humile* change as it displaces native ants, we measured isotopic ratios of Argentine ants over an 8-year period at an active invasion front in Rice Canyon (32°38′35′′ N, 117°01′15′′ W), a 78-ha coastal sage scrub site in Chula Vista, San Diego County, California (2). We used pitfall traps to sample ants along a transect oriented perpendicular to the front. The transect contained nine fixed sampling stations (each with five traps) placed every 120 m. Sampling took place in August/September each year between 1996 and 2003 (except for 1999, when no sampling occurred). Traps consisted of glass jars (6 cm in diameter) half full of ethylene glycol; traps were left open for 5 days during each sampling period. We stored all samples in 95% ethanol from collection until processing. Tillberg *et al.* (43) demonstrated that ethanol storage does not affect the δ^{15}N signature of ants. For each sampling station and year, we determined the δ^{15}N of a sample that consisted of heads, thoraces, and legs of 10–15 *L. humile* workers, such that sample dry masses weighed ≈1,500 μg. We weighed all samples into tin capsules and used a Mettler & Toledo microbalance to estimate mass. Analysis of nitrogen isotopic ratios was performed at the University of California, Davis, Stable Isotope Facility using a Europa Hydra 20/20 continuous-flow isotope ratio mass spectrometer.

To test whether the δ^{15}N values of Argentine ants changed as the invasion proceeded, we compared the δ^{15}N value for the first year that *L. humile* was recorded at a sampling station (i.e., at the leading edge of the invasion front) with the mean δ^{15}N value for that station in all subsequent years (i.e., after the displacement of native ants). For the nine fixed sampling stations, we used a paired *t* test to compare δ^{15}N values of Argentine ants at the front vs. those behind. This data set is unsuitable for repeated-measures ANOVA as a result of a missing year of data (1999) and the unfortunate loss of several samples during processing.

Biregional Comparisons of Trophic Ecology. We next analyzed stable isotope data on ants from six study sites in Argentina (native range) and California (introduced range) to quantify (*i*) how the trophic position of *L. humile* differs between native and introduced populations, and (*ii*) how the δ^{15}N values of Argentine ants compare with those of other syntopic ants. Sites in Argentina include three woodland/pasture locations along the Parana and Paraguay Rivers: (*i*) Reserva Natural Otamendi, Buenos Aires Province (34°13′30′′ S, 58°54′00′′ W), (*ii*) 6 km E Villa Ocampo, Santa Fe Province (28°30′30′′ S, 59°16′20′′ W), and (*iii*) 5 km E Herradura, Formosa Province (26°31′05′′ S, 58°16′50′′ W). Previous research at these sites (referred to as Otamendi, Ocampo, and Herradura) demonstrates that Argentine ants coexist with a diverse assemblage of native ants (28, 44). Sites in California include three scrub sites in San Diego County, California: (*i*) Otay-Sweetwater Unit of the San Diego National Wildlife Refuge (32°43′45′′ N, 116°56′30′′ W), (*ii*) University of California Elliot Chaparral Reserve (32°53′30′′ N, 117°06′10′′ W), and (*iii*) Torrey Pines State Reserve Extension (32°56′25′′ N, 117°14′55′′ W). Each of these sites (referred to as Sweetwater, Elliot, and Torrey Pines) varies in the extent of invasion by Argentine ants (2, 21, 45, 46). Sweetwater and Elliot contain large tracts of uninvaded scrub; *L. humile* is restricted either to riparian corridors (Sweetwater) or a *Eucalyptus* grove (Elliot). At Torrey Pines, a coastal site, Argentine ants occur nearly throughout the 100-ha reserve, and native ants are restricted to pockets of dry habitat unsuitable for Argentine ants (21).

At each site, we collected ants and other arthropods live into empty vials [with the exception of army ants (*Neivamyrmex*), which were collected into 95% ethanol (see ref. 43)]. For non-ant arthropods, we collected multiple herbivore and predator taxa. Herbivores included leaf feeders, such as larval Lepidoptera and adult Chrysomelidae, as well as phloem feeding Hemiptera. Predators were represented by spiders (Araneae: Lycosidae, Salticidae), scorpions, assassin bugs (Reduviidae), mantids, and beetles (Coccinellidae, Carabidae). We froze live arthropods and then dried them in a low-temperature oven at 45°C to 60°C. Finally, we collected leaves from common grasses, forbs, shrubs, and trees at each site to estimate the basal N-values of the primary producers in the above ground arthropod food web. Plant specimens were placed in sealed paper envelopes and then dried. After drying, all arthropod and plant samples were held in a sealed container with desiccant until processing.

Individual ant samples consisted of heads, thoraces, and legs of 10–15 workers from the same colony, such that sample masses were ≈1,500 μg. When possible, we sampled ants from at least five colonies per site per species

to incorporate intercolony variation in trophic level (43). Individual samples of non-ant arthropods were homogenized and weighed to $\approx 1{,}500$ μg per sample. Each plant sample was immersed in liquid N and ground into a fine powder using a mortar and pestle and weighed to $\approx 3{,}000$ μg. To obtain isotopic ratios, all samples were weighed and processed as described above under *Temporal Shifts in Trophic Position*.

To estimate the relative trophic position of *L. humile*, we used a single-isotope two food-source general mixing model (47); this statistic incorporates isotopic data from herbivorous and carnivorous arthropods from each site. First, we established a site-specific level of nitrogen enrichment, or trophic step (ΔN), rather than using a mean trophic step from the literature. We then calculated the relative proportion of dietary inputs to the ants from trophic levels $X-1$ (ρ_1) and X (ρ_2), where $\rho_1 + \rho_2 = 1$.

$$\rho_1 = \frac{(\delta^{15}N_{\text{ants}} - \delta^{15}N_{\text{predators}} - \Delta N)}{\begin{array}{c}(\delta^{15}N_{\text{ants}} - \delta^{15}N_{\text{predators}} - \Delta N + \\ \delta^{15}N_{\text{herbivores}} + \Delta N - \delta^{15}N_{\text{ants}}\end{array}}$$

Using these proportions, we estimate trophic position (TP) as follows:

$$\text{TP}_{\text{ants}} = \text{TP}_{\text{predators}} + 1 - (\text{TP}_{\text{predators}} - \text{TP}_{\text{herbivores}})\rho_1$$

where $\text{TP}_{\text{herbivores}} = 2$ and $\text{TP}_{\text{predators}} = 3$.

To analyze differences in trophic position between native and introduced ranges and among sites within each range, we performed a nested ANOVA with site nested within range. After ANOVA, we used Tukey comparisons to test for differences among sites.

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