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Plasticity in the trophic niche of an invasive ant explains establishment success and long-term coexistence

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Invasive species are one of the main threats to biodiversity worldwide and the processes enabling their establishment and persistence remain poorly understood. In generalist consumers, plasticity in diet and trophic niche may play a crucial role in invasion success. There is growing evidence that invasive ants, in particular, occupy lower trophic levels in their introduced range compared to the native one, but evidences remain fragmented. We conducted stable isotope analysis at five locations distributed on two continents to infer the trophic position of the invasive ant *Formica paralugubris* in the native and introduced part of the range. This species forms large colonies and can be a voracious predator while feeding on sugar-based resources as well. Whereas native populations had trophic positions comparable to that of an omnivore, the introduced populations varied from being honeydew specialists to top predators, or omnivore. Where other ant species co-occurred, there was no overlap in their trophic niches, and *F. paralugubris* occupied the lower position, suggesting that trophic displacement may enable the coexistence of different ant species. Taken together, our results suggest that shifts in diet associated with changes in the trophic niche of introduced species might mediate invasion success and enable long-term coexistence with native species.

Keywords: ants, impacts, invasive species, niche plasticity, stable isotopes, trophic level

Introduction

Invasive species are one of the primary threats to biodiversity and ecosystem functioning, due to their adverse effects on native communities (Bohan et al. 2017). One central question in invasion biology is whether some characteristics of introduced species might increase the probability they will successfully establish, spread and impact native communities (Ricciardi et al. 2017). In particular, the ability of species to adapt to the new conditions they encounter in their introduced range might be a



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key trait facilitating invasion. Indeed, shifts in the ecological niche occupied in the introduced range relative to the native range have been widely documented (Da Mata et al. 2010, Wei et al. 2017).

The ability of invasive species to shift their trophic niche is a fundamental aspect of invasion success, and there is evidence that trophic plasticity allows overcoming resource availability as an establishment constraint (Loureiro et al. 2019). Previous work indeed suggest that invasive species can shift their trophic niche in order to avoid interspecific competition and/or to adjust their diet to match resource availability in the invaded habitat (Grey and Jackson 2012, Jackson et al. 2012). As an example, the ecological success of invasive ants seems to be promoted by the association with honeydew producing Hemiptera in the introduced range (Styrsky and Eubanks 2007). This phenomenon was demonstrated in some globally invasive ants, like the red imported fire ant *Solenopsis invicta* (Wilder et al. 2011) and probably the yellow crazy ant *Anoplolepis gracilipes* (Wittman et al. 2018), that behaved like predators in their native range but became predominantly honeydew-consumers – thus becoming functionally herbivores – in their introduced range (Helms 2013). Also the Argentine ant *Linepithema humile* followed this pattern, though a certain variability in its trophic position was detected in different introduced areas (Tillberg et al. 2007).

In this study we investigate the trophic ecology of a red wood ant *Formica paralugubris* native to the Italian Alps and introduced to other parts of Italy and in Canada as biological control agent (Seifert 2016, Frizzi et al. 2020). Red wood ants (RWA) are a group of dominant ant species, widespread at high latitudes and altitudes in the Northern Hemisphere (Stockan et al. 2016). Recent investigations revealed that introduced populations of *F. paralugubris* are now becoming invasive (Seifert 2016, Frizzi et al. 2018).

We therefore aimed to 1) test whether the trophic positioning of *F. paralugubris* differs between its native and introduced range; 2) compare its trophic niche between its native and introduced range; 3) compare the trophic niche of *F. paralugubris* to that of other co-occurring ants. We expected the trophic positioning of *F. paralugubris* to be lower, and its trophic niche width to be smaller, in its introduced range compared to its native range. We also expected low overlap between the trophic niche of *F. paralugubris* and that of co-occurring species.

Material and methods

We conducted this study at five different sites: two in the Alps (Swiss National Park, Switzerland – SNP; Giovetto di Paline, Italy – GP), representing the native area, two in the Apennines (Abetone and Campigna, Italy – AB and CA) and one in Canada (Valcartier, Quebec – VC), representing the introduction areas (Supporting information).

Sampling was performed during summer 2017 (2018 for SNP). In each site, we randomly selected 10 *Formica paralugubris* nests, allowing a distance greater than 25 m from each

other, from which we collected 10 workers from the surface of nest mounds. To have reference points for ants' trophic positioning, at each site, we also collected herbivorous (caterpillars/grasshoppers, $5 < n < 32$) and predator (spiders, $8 < n < 20$) arthropods, samples of leaves of the dominant tree species and the most abundant herbaceous plant ($6 < n < 10$). Also, we collected workers of all other ant species we encountered. At CA and GP, we did not find any other ant in the area dominated by *F. paralugubris*, and samples were collected at the border of its population.

To remove potential biases due to ingested food, we removed gasters from ants and kept all the other arthropods alive for 24 h to let them empty their gut, before being killed by freezing. All samples were stored without any chemical at -20°C until they were dried in oven at 60°C for 48 h and ground to fine powder. Approximately 0.5 mg (for animals) and 2.0 mg (for plants) of each sample were packed into tin capsules and analysed using an isotope ratio mass spectrometer connected to an elemental analyser. One pool of 10 workers was analysed for each nest for each site.

Within each site, we obtained the trophic positioning of *F. paralugubris* by comparing its $\delta^{15}\text{N}$ values with those of herbivores and predators using Welch-corrected ANOVA, followed by Holm-corrected t-tests as multiple comparisons, where necessary. We calculated Layman's metrics (Layman et al. 2007) to compare intra-specific niche width: $\delta^{15}\text{N}$ range (NR) and $\delta^{13}\text{C}$ range (CR) as the differences between the most enriched and the most depleted individual, the total convex hull area encompassed by all individuals (TA), the mean Euclidean distance of each individual from the centroid of the $\delta^{15}\text{N}$ – $\delta^{13}\text{C}$ values (CD), the mean nearest neighbour distance in the $\delta^{15}\text{N}$ – $\delta^{13}\text{C}$ space (MNND), its standard deviation (SDNND) and the corrected standard ellipse area (SEAc), which is less biased from extreme values compared to TA (Jackson et al. 2011).

To test for differences among co-occurring ant species, we used PERMANOVA (Bray–Curtis dissimilarity, permutations = 4999), followed by t-tests with Benjamini–Hochberg p-value correction (Benjamini and Hochberg 1995) as multiple comparisons.

All statistical analyses were performed in R ver. 3.6 (<www.r-project.org>), using the packages SIAR (Parnell et al. 2010) and vegan (Oksanen et al. 2020).

Results

At all sites, we found a significant difference among the $\delta^{15}\text{N}$ of all groups (SNP: $F_{2,28,61} = 253.7$, $p < 0.001$; GP: $F_{2,12,18} = 53.50$, $p < 0.001$; AB: $F_{2,15,64} = 511.78$, $p < 0.001$; CA: $F_{2,17,33} = 82.81$, $p < 0.001$; VC: $F_{2,9,88} = 152.71$, $p < 0.001$; Fig. 1). More specifically, in both native areas, the $\delta^{15}\text{N}$ for *Formica paralugubris* were intermediate between those of herbivores and predators, and significantly different from both ($p < 0.001$). In the introduction areas, however, a more complex pattern emerged. At CA, similarly to native areas, *F. paralugubris* showed $\delta^{15}\text{N}$ intermediate between

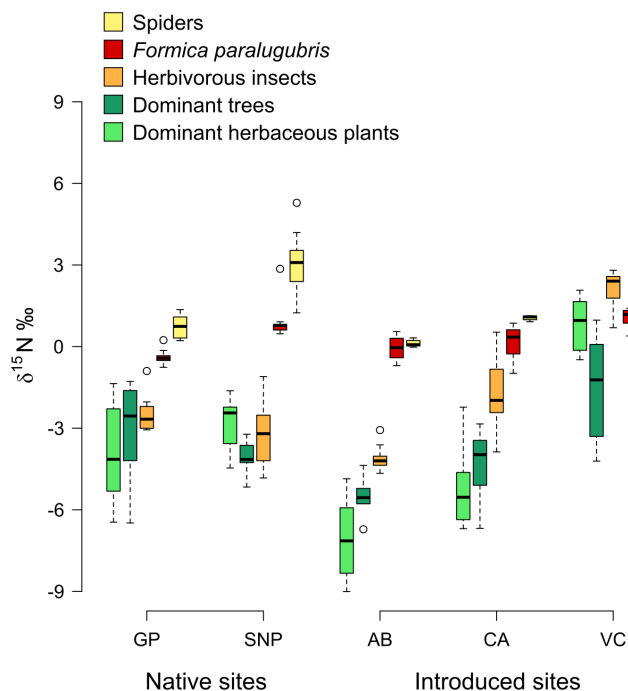


Figure 1. $\delta^{15}\text{N}$ (‰) of sampled groups in all sites. GP = Giovetto di Paline (Italy); SNP = Swiss National Park (Switzerland); AB = Abetone (Italy); CA = Campigna (Italy); VC = Valcartier (Canada).

those of herbivores and predators, and distinct from both ($p < 0.001$). At AB, the $\delta^{15}\text{N}$ of *F. paralogubris* were significantly higher than that of herbivores ($p < 0.001$), but equal to that of spiders ($p = 0.20$). Finally, at VC, *F. paralogubris* $\delta^{15}\text{N}$ were significantly lower than that of spiders ($p < 0.001$), and lower, although marginally not significant ($p = 0.06$), than that of herbivores.

We found no relationship between the intra-specific niche width and the autochthonous/introduced status of the populations, or their trophic positioning (Table 1). The nitrogen range was highest at SNP followed by Campigna, and lowest at Giovetto and Valcartier; the carbon range was highest in Abetone and lowest in Valcartier; the total area was highest in Abetone and Campigna, and lowest in Valcartier.

Table 1. Layman's metrics for *Formica paralogubris* populations. NR ($\delta^{15}\text{N}$ range) and CR ($\delta^{13}\text{C}$ range) are the differences between the most enriched and the most depleted individual; TA is the total convex hull area encompassed by all individuals; CD is the mean Euclidean distance of each individual from the centroid of the $\delta^{15}\text{N}$ - $\delta^{13}\text{C}$ values; MNND and SDNND are the mean nearest neighbor distance in the $\delta^{15}\text{N}$ - $\delta^{13}\text{C}$ space and its standard deviation; SEAc is the corrected standard ellipse area.

Site	NR	CR	TA	CD	MNND	SDNND	SEAc
Giovetto di Paline (GP)	1.0	1.0	0.5	0.4	0.2	0.1	0.3
Switzerland (SNP)	2.4	0.5	0.7	0.5	0.3	0.6	0.5
Abetone (AB)	1.3	1.3	0.8	0.5	0.2	0.1	0.5
Campigna (CA)	1.8	0.7	0.8	0.5	0.3	0.2	0.5
Valcartier (VC)	1.0	0.3	0.2	0.3	0.2	0.1	0.1

Comparable values were obtained for centroid distance and mean nearest neighbour distance, while the standard deviation of the mean nearest neighbour distance was highest in Switzerland and lowest in Abetone and Valcartier. The corrected standard ellipse area confirmed the total area results, being highest in Abetone and lowest in Valcartier.

Other co-occurring ant species were found only at SNP and VC, while in all the other sites other ant species were only found at the edge of *F. paralogubris* dominated area. In Switzerland and Canada, *F. paralogubris* had an isotopic niche clearly segregated with respect to the native *Formica exsecta* ($F_{1,18} = 68.22$, $p < 0.001$) and *Formica glacialis* ($F_{1,12} = 121.15$, $p < 0.001$), respectively. Differences were evident in both sites for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ($p < 0.001$ for each test), with *F. paralogubris* having lower $\delta^{15}\text{N}$ and higher $\delta^{13}\text{C}$ (Fig. 2). In Italy, ants were overall statistically differentiated at GP ($F_{4,15} = 4.25$, $p < 0.05$), but not at AB ($F_{3,14} = 2.26$, $p = 0.13$) and CA ($F_{6,30} = 1.95$, $p = 0.05$). In particular, in GP post hoc test found a significant difference between *F. paralogubris* and other ants of the genus *Formica*, *Myrmica* and *Lasius* ($p < 0.05$ for all), while no differences were found between *F. paralogubris* and *Camponotus* ($p = 0.09$) (Supporting information).

Discussion

Among several mechanisms determining the success of invasive species is the plasticity of their diet or trophic niche (Linzmair et al. 2020, Rolla et al. 2020). We show that the trophic positioning of invasive ants can change in response to local conditions. We observed considerable inter-population variability in trophic positioning of *Formica paralogubris* suggesting trophic niche plasticity. Our results suggest that invasive species can adapt to resource availability and/or interactions with other co-occurring species in the introduced range by switching diet.

Within its native range, *F. paralogubris* behaved like an omnivore, supporting the literature demonstrating that RWA rely on both animal preys and aphid honeydew (Domisch et al. 2016), even if one species was found to be a first-order predator (Iakovlev et al. 2017), suggesting that generalizations are hardly possible for this group.

Isotopic values of introduced populations of *F. paralogubris* suggest that invasive ants can adopt behaviours ranging from being omnivore to being specialized predators or herbivores. In line with our expectations, the Canadian population occupied a trophic positioning of an exudate-feeding herbivore, indicating an almost complete reliance on aphid honeydew (Brewitt et al. 2015). Indeed, invasive ants are known to form association with honeydew-producing insects in their introduced range which lower their trophic position. Introduced *L. humile* decreased their trophic level compared with native populations, with a shift from predatory habits to greater consumption of plant-derived sources (Tillberg et al. 2007). This result was confirmed for *S. invicta*, whose colonies supplied with aphids' honeydew were also significantly denser

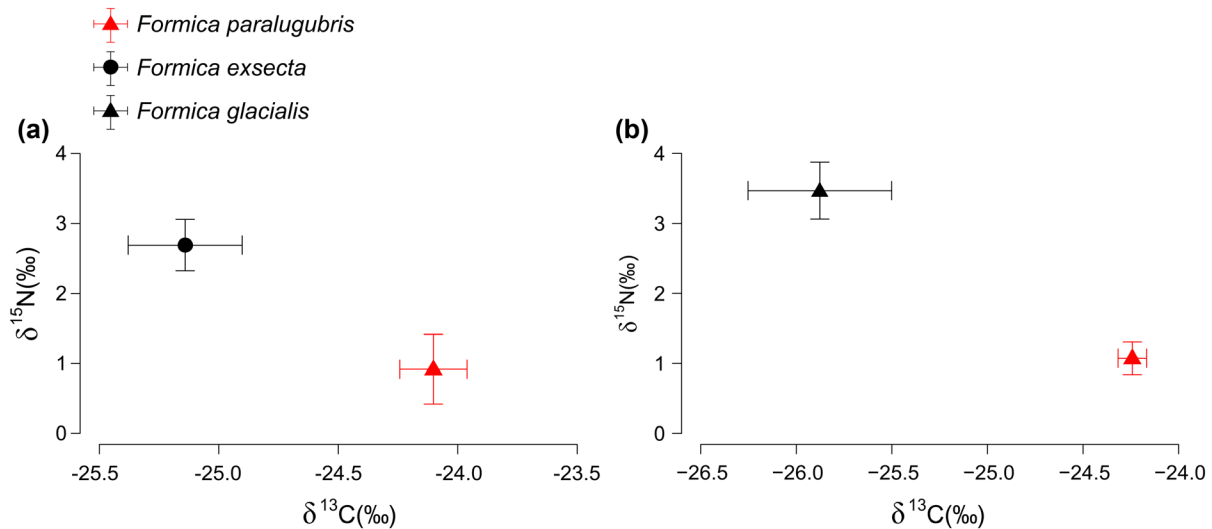


Figure 2. Isotopic biplot (mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C} \pm \text{SE}$) for: (a) SNP (Swiss National Park, Switzerland) and (b) VC (Valcartier, Canada).

than controls (Wilder et al. 2011). Similar results were found also for *A. gracilipes*, whose $\delta^{15}\text{N}$ in invasive populations was negatively correlated with ant density (Wittman et al. 2018).

Two explanations have been postulated to explain the decrease in trophic position in invasive ants: the resource preference hypothesis (RPH) and the resource limitation hypothesis (RLH). According to RPH, invasive ants feed on their preferred source (carbohydrates) due to the lack of strong competitors. According to RLH, the shift is a consequence of the reduced availability of other preferred preys (Shik and Silverman 2013). *Solenopsis invicta*, which in the invaded range monopolized sugar-rich resources, seems to support the RPH (Wilder et al. 2011), while *L. humile*, which lowered its trophic level during its invasion history as a result of prey selection, seems to confirm the RLH (Tillberg et al. 2007). Whether the observed shift in the Canadian population of *F. paralogubris* follows the former or the latter hypothesis is not clear, even if evidence in favour of RPH is stronger. Indeed, in Valcartier *F. paralogubris* coexists with the native *F. glacialis*, which relies more on animal preys as indicated by its higher $\delta^{15}\text{N}$ values, suggesting that prey availability may not be an issue here. Moreover, aphid populations markedly increased after the introduction of *F. paralogubris* to Valcartier (McNeil et al. 1977).

The other introduced populations showed varying behaviours. The Campigna population exhibited omnivorous habits, while the Abetone population exhibited predatory habits. At Campigna, no other ant species coexist with *F. paralogubris*, making interspecific competition unlikely, and arthropod populations are depleted by ant predation (Frizzi et al. 2018). Though no information on the status of arthropod assemblages is available for Abetone, competitive exclusion of other ants seems to be less stringent, because in this site some small ant nests occur where *F. paralogubris* density is lower. However, competition with these sparse and small colonies cannot explain the lower reliance on aphid exudates. This variability in the trophic positioning of introduced

populations reflects that found for *L. humile*, which showed herbivorous, omnivorous and predatory habits in different invaded sites (Tillberg et al. 2007).

The analysis of the trophic niche did not reveal any clear pattern related to the autochthonous/introduced status nor the trophic positioning of the populations. This was true for the metrics resuming either the carbon and nitrogen variability (i.e. carbon range and nitrogen range) as well as the isotopic niche area (e.g. total area and corrected standard ellipse area). In Valcartier, we recorded the highest degree of trophic specialization of *F. paralogubris* (expressed by the narrowest nitrogen range, carbon range, total area and corrected standard ellipse area). The narrow nitrogen range suggests the consumption of a single N source, and the narrow carbon range suggests feeding on a few aphid species on a limited number of plant species, since honeydew reflects phloem isotopic signature (Sagers and Goggin 2007). This specialization could reflect the exclusion of native ants from carbohydrate resources, supporting previous results (Tillberg et al. 2007, Wilder et al. 2011). In contrast, the Swiss population showed the wider nitrogen range values, suggesting the consumption of preys belonging to different trophic levels. Interestingly, some inter-colonial differences in trophic behaviour were found in the native range, as found in *S. invicta* (Roeder and Kaspari 2017).

We found coexistence with other species only at a few sites. At Valcartier and in Switzerland, *F. paralogubris* coexisted with *F. glacialis* and *F. exsecta*, respectively. These species had isotopic values completely separated, suggesting niche partitioning and likely avoiding exploitative competition. At both sites, *F. paralogubris* had a lower trophic positioning than the native species and fed on different carbon sources. At all the other sites, *F. paralogubris* apparently excluded most of the other ants, at least from the areas where its population density is higher (Frizzi et al. 2018). An overall trophic niche segregation was found in Giovetto, while in the Apennines all other ants had overlapping niches with *F. paralogubris*.

However, interspecific competition is likely reduced by spatial segregation.

In conclusion, the expected decrease in trophic position of the introduced populations of *F. paralugubris* is not always supported by our findings. Instead, this species demonstrated considerable trophic plasticity, being able to adapt to different ecological scenarios, supporting the importance of trophic plasticity as a key feature of invasive ants (Suehiro et al. 2017) and other species (Jackson et al. 2017). Our results show that generalizations on trophic shift in invasive species are much more difficult than previously thought. As such, further investigation on a wider range of taxa are required to investigate whether the absence of clear directional trends is a feature of this particular species or is a more common but neglected phenomenon among invasive species. Moreover, evaluating whether species exhibiting dietary plasticity are more likely to become invasive and impact several trophic levels in the invaded communities through competition and predation will be a promising research avenue. Lastly, it will be interesting to expand this line of research to other ecosystems and look for spatiotemporal variations in invasive species' trophic plasticity, for example across the invasion stages.

Data availability statement

Data available from the OSF repository: <www.osf.io.yjpcw> (Balzani et al. 2021).

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Author contributions

Paride Balzani: Conceptualization (equal); Formal analysis (lead); Investigation (equal); Writing – original draft (lead). **Salvatrice Vizzini:** Resources (equal); Writing – review and editing (equal). **Filippo Frizzi:** Investigation (equal); Writing – review and editing (equal). **Alberto Masoni:** Investigation (equal); Writing – review and editing (equal). **Jean-Philippe Lessard:** Investigation (equal); Writing – review and editing (equal). **Christian Bernasconi:** Investigation (equal); Writing – review and editing (equal). **André Francoeur:** Investigation (equal); Writing – review and editing (equal). **Javier Ibarra-Isassi:** Investigation (equal); Writing – review and editing (equal). **François Brassard:** Investigation (equal); Writing – review and editing (equal). **Daniel Cherix:** Investigation (equal); Writing – review and editing (equal). **Giacomo Santini:** Conceptualization (equal); Investigation

(equal); Supervision (lead); Writing – review and editing (equal).

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