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*Research article*

# Native ants learn how to deal with cues of invasive species: responses to footprints of invasive ants are shaped by experience


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Invasive ants threaten biodiversity worldwide. They may benefit from being novel if native species fail to show appropriate responses to their cues. Cues include chemical footprints (or 'home-range markings' in ants) left by all walking insects, which resemble cuticular hydrocarbons (CHCs). Ants are known to rely heavily on such cues to forage and recognise other individuals. We investigated the response of *Lasius niger* ants in central Europe to cues of two invasive ant species (*Lasius neglectus* and *Linepithema humile*), studying whether they were shaped by experience and whether the ants discriminated between cues of different species. Groups of *L. niger* workers encountered invasive ant workers in a negative (aggressive), positive (food-associated), or neutral (neither aggression nor food) context. Using Y-mazes with one blank arm and one arm with footprints, we investigated how this affected their response to footprints compared to responses of naïve ants. Naïve *L. niger* avoided footprints of both species, walking on the cue-bearing Y arm less than expected by chance (42.9 ± 0.6% SE versus 50% choosing the cue-bearing arm). Avoidance became stronger after negative encounters (35.3 ± 1.9%). However, their response did not change significantly after neutral encounters, whereas they approached the footprints after positive experience (62 ± 1.3% choosing the cue-bearing arm). Notably, there was no change in response to footprints of a species they had not encountered. Our results show that ants can link individual experience with living ants to their chemical footprints, thus transferring information between contexts. Also, they learn to respond specifically to cues of certain species, but do not generalise

**Synthesis**

Many animals use chemical cues left by others to gauge the risk of encountering competitors or predators. This ability can give invasive species and advantage, especially if native species fail to recognize or respond to these cues. However, such advantage may only exist if the cue recognitions is hardwired. This is because if native species can learn to associate those cues with danger or opportunity through experience, they may quickly adapt their behaviour and reduce the invader's advantage. In our study, we show that native ants *Lasius niger* can learn to recognize and respond appropriately to the chemical footprints of two invasive ant species. After aggressive encounters, the ants avoided areas marked by their invader. However, when those encounters occurred near food, they were more likely to return. These findings reveal that ants adjust their behaviour based on experience, using both positive and negative associations to fine-tune their foraging strategies and reduce associated risks.

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their responses to cues of other species. Ants hence might learn to interpret the wealth of chemical cues in their environment and use it to optimise foraging decisions. At least for other ants, invasive ants may not benefit from being novel.

Keywords: foraging behaviour, non-consumptive effects, Formicidae, cuticular hydrocarbons, antipredator behaviour, interspecific competition

## Introduction

Invasive species are a major threat to biodiversity (Clavero and García-Berthou 2005). In many cases, their success is partly due to the fact that native species are not adapted to the invader and do not show appropriate responses (Carthey and Banks 2014). This has been mainly studied in the context of predator–prey interactions, but also applies to competitive interactions. For example, prey individuals may fail to recognise invasive predators or their cues as threat, but also predators may fail to prey on invasive species ('predator–prey naïveté', Cox and Lima 2006, Sih et al. 2010). Such novel species interactions are part of the reason why alien predators often cause stronger reductions of prey populations than native predators (Salo et al. 2007, Paolucci et al. 2013). Prey individuals which recognise predator cues often perform anti-predator behaviour. This includes hiding, freezing, or enhancing/reducing their movement speed, and has been shown in a wide range of taxa, including toads, spiders, aphids and crickets (Persons et al. 2002, Gonzalo et al. 2008, Ninkovic et al. 2013, Cisterne et al. 2014, Binz et al. 2014a, Bucher et al. 2014). It can lead to strong non-consumptive effects of predators on prey, which cascade down to other trophic levels (Bucher et al. 2015, Suraci et al. 2016). Anti-predator behaviour is often specific to predator species, with prey responding most to cues of common or particularly dangerous predators (Binz et al. 2014a, Mestre et al. 2020). Invasive predators benefit from naïve prey that fail to show anti-predator behaviour (Brown and Warburton 1999, Cox and Lima 2006). For example, aphids tend to avoid footprints of native ladybeetle predators, but ignore invasive ladybeetles (Bertleff et al. 2021).

Next to predator–prey interactions, competition is a major problem caused by invasive species, although cue-mediated effects have been studied much less in this field. In this context, ants are a particularly important taxon. Firstly, many ant species are invasive around the globe, with five of the 100 worst invasive species being ants, including *Linepithema humile, Solenopsis invicta, Wasmannia auropunctata, Pheidole megacephala* and *Anoplolepis gracilipes* (Invasive Species Specialist Group (ISSG) 2025). Invasive ants can outcompete native ant species, thus strongly reducing richness of native ant communities; for example, no ant species have been found to coexist with *Lasius neglectus* in its invaded range (Holway et al. 2002, Sanders et al. 2003, Wittman 2014). Secondly, ants are ubiquitous in nearly all terrestrial ecosystems (Schultheiss et al. 2022) and are important predators or competitors for other arthropods (Sanders and Platner 2007). Finally, ants themselves use chemicals for orientation and communication. Thus, they may cause anti-predator behaviour based on various cues they produce, in prey species (Mestre et al. 2014, 2020), but also themselves respond to chemical cues of other species, such as competing ants.

For ants, the worst enemies are not predators, but other ants (Hölldobler and Wilson 1990). This is because in ants, competition plays a central role for intra- and interspecific interactions. Aggressive interactions in the context of food competition are ubiquitous and central in structuring ant communities. Usually, there are dominant species which aggressively combat and displace subdominant or subordinate species at food resources (Cerdá et al. 2013, Menges et al. 2024), and this way monopolise food sources (Parr and Gibb 2010, Drescher et al. 2011). This can even lead to ants being killed by competitors, both in intraspecific (*Tetramorium*: Seifert 2018) and interspecific interactions (Holway 1999, Morrison 2000, Menzel et al. 2008b, Binz et al. 2014b). Therefore, some species of ants and other eusocial insects, but also of mammals, avoid cues of potential competitors, showing 'anti-competitor behaviour'. *Lasius niger* ants avoid chemical footprints of other conspecific colonies (Wüst and Menzel 2017), which represent competitors, and certain subordinate ants avoid cues of dominants (Binz et al. 2014b). Bumblebees avoid flowers where others have been before (Wilms and Eltz 2008), and some stingless bees avoid recruitment pheromones of a competing species (Lichtenberg et al. 2011). Moreover, a vole species was shown to avoid scent marks of a competing species under high predation risk (Hughes et al. 2010).

However, some species of ants, bumblebees and stingless bees show the opposite response. They eavesdrop on foreign cues to exploit food sources discovered by another species (Nieh et al. 2004, Menzel et al. 2010a, 2010b, 2014, Wilms and Eltz 2008, Powell et al. 2014). Like competitor avoidance, such eavesdropping is not only restricted to eusocial insects. For example, some bird or bat predators locate their prey by eavesdropping on their mating calls (Tuttle and Ryan 1981, Igaune et al. 2008), and many other arthropods eavesdrop on ant signals to locate either food sources or the ants themselves (Adams et al. 2020). Finally, some bat species eavesdrop on other species' echolocation calls and approach their sources (Übernickel et al. 2013).

In ants, the cues involved in eavesdropping or avoidance are often trail pheromones, but in some cases also chemical footprints (Binz et al. 2016, Wüst and Menzel 2017). Chemical footprints are tiny hydrocarbon droplets left unintentionally by any walking insect. They are secreted by the tarsal arolium, probably to enhance foot adhesion. Footprints have a similar (albeit not equal) composition to cuticular hydrocarbons and are therefore species-specific (Geiselhardt et al. 2011, Wüst and Menzel 2017). Thus, they convey reliable information on the recent presence and activity of the species which left them. In ants, footprints of nestmates serve as home-range



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markings (Lenoir et al. 2009), helping individual workers to assess their own distance from the nest (Devigne and Detrain 2006). Since footprint densities indicate local worker density and/or activity (Devigne et al. 2004), using footprints as cues to modulate own behaviour can be advantageous. Indeed, they can modulate worker movement (Devigne and de Biseau 2012, Wüst and Menzel 2017) and foraging behaviour (Devigne et al. 2004, Popp and Dornhaus 2024), also in concert with trail pheromones (Akino and Yamaoka 2005). Compared to nestmate footprints, the use of cues from other colonies and species was studied much less, although some ants clearly respond to chemical footprints of other colonies or species, including non-ants. Foreign cues are often approached (suggesting eavesdropping), but some species, including *Lasius niger,* also avoided footprints of other colonies or other species (Binz et al. 2016, Wüst and Menzel 2017, dos Santos et al. 2024).

Responses to other species' cues, be it competitor/predator avoidance or eavesdropping, should be fine-tuned to the co-occurring species in the individual habitat and their competitive abilities. Genetically fixed adaptations would likely be too slow to allow fine-tuned responses to predator or competitor communities that may fluctuate quickly in space and time. Hence, an insect would greatly benefit if it could learn which cues should be avoided and which cues indicate species that might be eavesdropped on, for example if they tend trophobionts or discovered other rich food sources. In the context of species invasions, this ability may be vital to counteract predator-prey naïveté or competitor naïveté (Sih et al. 2010), i.e. native species should be able to learn appropriate responses to cues of invasive species via associative learning. As outlined above for novel predators, invasive species can benefit from being novel if native species do not respond to their cues, e.g. failing to avoid their cues if the invasive species is a superior competitor.

Ants can learn CHCs of other species (Hojo et al. 2014, van Wilgenburg et al. 2010), but we are not aware of studies investigating whether ants can link information from CHCs and chemical footprints. The question of whether ants can use their experience with living or dead heterospecific ants to perform appropriate responses to footprints of these ant species becomes a crucial issue in the context of species invasions, with implications for conservation biology. An invasive predator or competitor will have less deleterious impacts on native species if they can learn to avoid their cues. Despite many studies on associative learning in ants or other insects, to our knowledge, no study so far tested whether ants or other insects can transfer information about other insect species to their chemical footprints. Also, to our knowledge it has not yet been studied whether ants, after negative experience with another species, would avoid footprints of this species specifically, would avoid all chemical footprints of any other species, or would not respond to their chemical footprints at all because it did not establish the link between the aggressive insect and its footprints. This question is relevant both in competitive interactions and in predator-prey interactions.

Therefore, we investigated behavioural responses of *Lasius niger* ants to cues of two invasive ants, *L. neglectus* and *L. humile*, and tested whether these responses can be modified by positive (food-associated, see below in 'Experimental design'), neutral or negative (aggressive) experience. We studied the responses 1 h and 48 h after encountering the invasive species, to investigate effects on short-term memory (1 h) and long-term memory (48 h) (Piqueret et al. 2019). *Lasius neglectus* is invasive in Germany, and inhabits urban or semiurban habitats similar to those colonised by *L. niger*, but displaces all other ant species. *Lasius humile* is listed among the worst 100 invasive organisms worldwide. It has devastating effects on native ant faunas and is probably the most detrimental invasive ant in Europe to date (Giraud et al. 2002, Wittman 2014). In Germany, it is not yet established despite occasional reports of local colonies (G. Heller pers. comm.).

## Material and methods

### Ant species, collection and maintenance

The black garden ant *Lasius niger* (Formicidae: Formicinae) is native to Europe and parts of Asia, and common in agricultural and suburban habitats. It is aggressive towards other ants, including conspecifics. Colonies are monogynous and monodomous and can have up to 40 000 workers (Seifert 2018).

Fifteen colony fragments of *Lasius niger* were collected in summer 2022 near Mainz, Germany (49°59'N, 08°13'E). We only considered nests at least 4-6 meters apart from each other. Each colony fragment was collected and, together with nest soil, transferred to plastic boxes with fluon-coated walls and a plastered floor. The ants were given water ad libitum and were fed thrice a week with honey and dead crickets. All colony fragments were queenless, had 400 to 900 workers and around 50 to 150 larvae. All experiments were done within eight weeks after collection of the *L. niger* colony fragments.

*Lasius neglectus* was described only recently (van Loon et al. 1990). It is invasive in many regions of Europe, especially in urbanised habitats that represent potential habitats for *L. niger*, and can form supercolonies (Cremer et al. 2006, Seifert 2018). The closest *L. neglectus* occurrence to our *L. niger* collection site is a population ca 50 km away. We collected *L. neglectus* workers in May 2022 from a supercolony in Jena, Germany.

The Argentine ant *Linepithema humile* (Formicidae: Dolichoderinae) has been introduced to southern Europe decades ago (Giraud et al. 2002). It was reported from Germany only sporadically, and never close to Mainz. To date, *Li. humile* populations frequently die out again during winter (G. Heller pers. comm. 2024). Thus, our *L. niger* colonies had never encountered either invasive species. For our study we used *Li. humile* collected in January 2022 from a supercolony close to the Mediterranean Sea (Hyères, France). Of both invasive species, we kept worker groups with queens and brood items. Both *L. neglectus* and *Li. humile* are highly aggressive towards other ant species, can displace and outcompete native ants and thus severely reduce abundance and diversity of native ant communities (Human and Gordon 1999, Wittman 2014, but see Cordonnier et al. 2020, Invasive Species Specialist Group (ISSG) 2025).



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## Experimental design

To test whether footprint responses are plastic and depend on the ants' experience, we created six groups of 10 workers each from each *L. niger* colony fragment (foragers only). The groups were then assigned to either positive, neutral or negative encounters, either with *L. neglectus* or *Li. humile*, totalling 3 × 2 = 6 treatments (Fig. 1). As positive encounters, ants were confronted with dead invasive ants together with sugar. This setting was to mimic one of two natural scenarios. Firstly, it could mimic non-aggressive interactions of ants at a food source, such as a trophobiont (such as an aphid) that produces honeydew. Only some aphid species produce honeydew and are tended by ants, and earlier studies showed that ants can discriminate myrmecophilous and non-myrmecophilous aphid species based on their CHCs (Lang and Menzel 2011). Secondly, the setting could represent a competitively inferior ant (thus no aggression) foraging at a food source. Aggressive take-over of food sources by other, usually competitively superior ant species is ubiquitous in nature (Cerdá et al. 2013). Thus, both options represent situations where cuticular hydrocarbons (or other cues) can be associated to food (such as carbohydrates). Note that ants and other arthropods often respond to chemical cues irrespective of whether the cue-bearing object is alive or dead (van Zweden and d'Ettorre 2010). Neutral encounters were similar as above, but did not include sugar. Finally, negative encounters were confrontations with living invasive ants, which attacked and sometimes killed some of the *L. niger* workers.

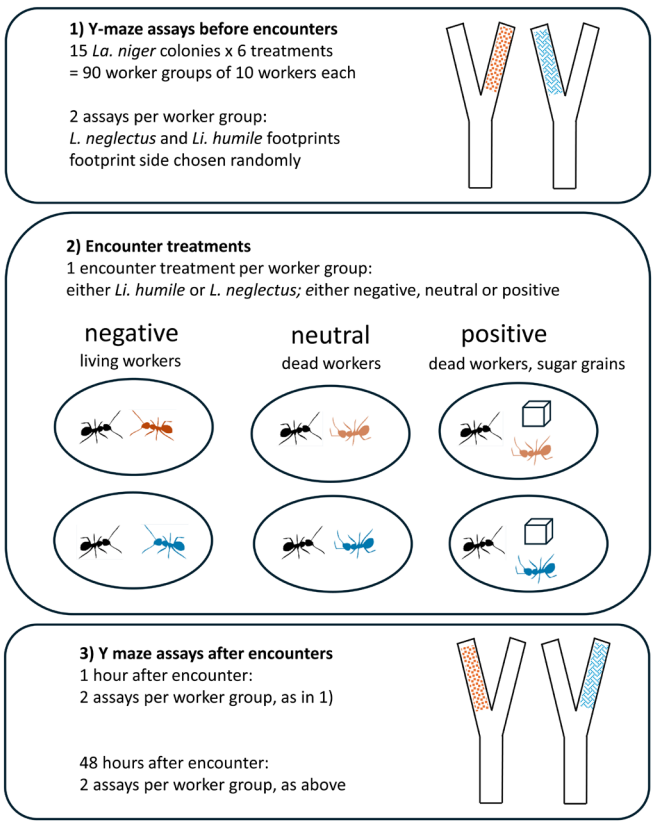


Figure 1. Overview of the experimental setup.

Using Y-mazes, we tested the response of the workers to footprints of both *L. neglectus* and *Li. humile* before the encounters, 1 h thereafter (to test short-term memory) and 48 h thereafter (to test long-term memory). Thus, each worker group was tested six times (3 time points × 2 invasive species = 6 Y-maze assays), yielding a total of 540 Y-maze assays (15 colony fragments × 6 treatments × 6 assays per worker group). Between the 1 h and the 48 h assays, they were kept at 21°C with honey and water ad libitum. All experiments were performed between June and September 2022. The worker groups were acclimated for 1–2 h before the experiment, such that they had been separate from their colony fragment only for ca 2 days at the end of the assays. No ethical approval was necessary to perform these experiments.

## Y-maze assays

On paper Y-mazes, we tested whether the ants preferred to walk on paper with or without footprints. We always used one Y-maze with *L. neglectus* footprints and one with *Li. humile* footprints in a randomised order and a break of 10 minutes in between (Fig. 1). The Y-mazes had a 7 cm long basis and 9.5 cm long arms. One arm contained footprints. The side of the cue-containing arm was varied haphazardly (for each treatment, 45 replicates each with footprints on the right and the left side, respectively), and the observer was blind as to which arm contained footprints. To obtain footprints, we placed fluon-coated PVC frames (7.5 × 2.4 cm; 2 cm high; without floor) on both arms of the Y-maze. Then 15 workers of either *Li. humile* or *L. neglectus* were placed into one of the frames, the other one remaining empty. The ants were allowed to walk around within the frame for one h, thereby leaving footprint hydrocarbons. Each maze was used for one assay only and prepared one h before the assay. It was then placed on a fluon-coated scaffold such that the two Y arms pointed upwards. All ten ants were allowed to enter the maze singly, and only after the previous ant had been gently removed with soft forceps. We recorded whether they decided for the cue-free or the cue-bearing arm of the Y, and considered a decision final when the ant had crossed the 'line of no return' 1 cm behind the bifurcation. Usually, the ants decided for an arm within 5 s.

## Encounter treatments

Encounters took place in fluon-coated circular arenas (8 cm diameter) with paper floor. Each worker group experienced two similar encounters of 2 min each, with a break of 5 min in between. In negative encounters, the *L. niger* worker groups were confronted with eight living workers of either *Li. humile* or *L. neglectus.* Preliminary tests had shown that ten *Li. humile* or *L. neglectus* workers resulted in too many *L. niger* deaths and thus too few survivors for our experiments. In contrast, both invasive species suffered much fewer casualties than *L. niger*, with one killed *L. neglectus* or *Li. humile* workers at maximum, even in the preliminary assays of 10 invasive:10 *L. niger* workers. Especially *Li. humile* was highly aggressive in the assays and was killed very rarely.



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First, eight *Li. humile* or *L. neglectus* workers were placed into the arena. After 10 min, 10 *L. niger* workers were added. Usually, the two species engaged in fights. After two minutes, *Li. humile* or *L. neglectus* were removed from the arena, and added again after five min. We did this to simulate two encounters. After the second encounter, the *L. niger* workers were gently transferred to a small plastic box with honey and water ad libitum and allowed to rest before Y-maze assays. Both *Li. humile* and *L. neglectus* were highly aggressive and frequently killed *L. niger* individuals. The final number of surviving *L. niger* was 7.67 ± 0.15 SE workers (median: 8). If *Li. humile* or *L. neglectus* were killed during the first encounter, their numbers was replenished to 8 for the second encounter in order to have the same number of aggressors in both encounters. The *L. niger* groups were not replenished so that all workers of the groups would have the same level of experience.

For positive encounters, the *L. niger* groups were confronted with dead invasive ants together with sugar. We used granular sugar because any aquaeous solution might have concealed or altered the ant footprints. The *L. niger* workers were placed into the arena for 10 min. Then, they were presented eight dead (frozen and defrosted) workers of either *Li. humile* or *L. neglectus* together with ca 2 g of sugar on a small metal plate (2.5 cm diameter) for 2 min. The plate was removed after 5 min and replaced into the arena for 2 min. After that, *L. niger* was transferred to a plastic box as above. For neutral encounters, we presented dead workers as above, but without sugar. Thus, the ants encountered the invasive ants without any negative or positive consequences.

### Statistical analysis

For each Y-maze assay, we calculated the ratio of ants that chose the footprint-bearing arm compared to all ants that chose any arm (i.e. 7–10 workers, depending on whether workers were killed) ('decision ratio'). A ratio below 0.5 indicated that more ants had chosen the cue-free arm, while a ratio above 0.5 indicated that more ants had chosen the footprint arm. In few cases, individual ants took more than 10 seconds to cross the line of no return, suggesting low activity. These individuals represented 2.89 ± 0.24% SE of all individuals (2.3–3.1% per treatment) and were excluded from the dataset before further analysis.

To analyse short-term effects of the encounters with invasive ants, we calculated the difference between the decision ratio 1 h after the encounters and the ratio before the encounters, separately for each worker group and each invasive species. A difference below 0 indicated that the workers avoided the footprints more strongly than before the confrontation ('avoided' being defined here as 'chosen less than expected by chance'), while a difference above 0 indicated that workers approached them more than before. These differences were analysed with a linear mixed-effects model (*lmer*, R packages 'lme4' and 'lmerTest' (Bates et al. 2014, Kuznetsova et al. 2017). The independent variables were *encounter type* (positive, neutral or negative), the species the footprints stemmed from (*footprint species*), the species the ants encountered (*encountered species*), and the information whether *footprint species* and *encountered species* were identical ('*FP = encountered species*'). Two-way interactions of encounter type with the three other variables were allowed. We chose to create the variable '*FP = encountered species*' (true or false) since we were only interested in this dichotomy. Allowing the *interaction footprint species:encountered species* instead would have reduced statistical power and made the model unnecessarily complex by creating four factor levels instead of two. *Colony ID* and worker group ID of the *L. niger* ants were included as nested random intercept. The models were analysed with a likelihood test (command Anova, R package 'car' (Fox and Weisberg 2019); for specific effects of *encounter type*, *t* values and their corresponding p values were obtained from model summaries. Binomial models were created for comparison and yielded very similar results, but violated several model assumptions and therefore were not further used (Supporting information).

Similar analyses were conducted for the long-term responses 48 h after the encounters. Furthermore, we ran an analogous model for the footprint responses before the encounters after subtracting the expected value of 0.5 from all ratios. This was to analyse potentially innate responses to any of the footprints, but also to check whether the behaviour of the worker groups showed any random differences among their assigned treatments. For comparison, we also analysed footprint responses without subtracting 'naïve' decision ratios before the encounters (Supporting information). Finally, we analysed a comprehensive model of corrected decision ratios, which included responses after 1 h and after 48 h (Supporting information). All analyses were done in R ver. 4.2.0 (www.r-project.org).

## Results

### Response to footprints before the encounters

Before the encounters, *L. niger* avoided footprints from the two invasive species, i.e. they approached Y arms with footprints less often (42.9 ± 0.6% SE) than expected by chance (50%) (Fig. 2). Ants avoided footprints of *Li. humile* (difference from random expectation: $t = -3.181$, $p = 0.0019$), and even more those of *L. neglectus* ($t = -5.55$, $p < 0.0001$). The decision ratio differed between the two invasives (*footprint species* $\chi^2_1 = 15.32$, $p < 0.0001$, 40.7 ± 1.0% versus 45.1 ± 0.8%), but did not differ between the assigned encounter treatments (Table 1, Supporting information).

### Short-term responses

The confrontation treatments had a strong effect on how the workers responded to footprints. Workers approached footprints significantly more after positive experience with invasive ants, and avoided them significantly more after negative encounters with the respective ant species (positive experience: 62 ± 1.3% approaching the footprint arm, which is an increase of 19.4 ± 2.3% compared to the naïve ants; negative experience: 35.3 ± 1.9% approaching the footprint



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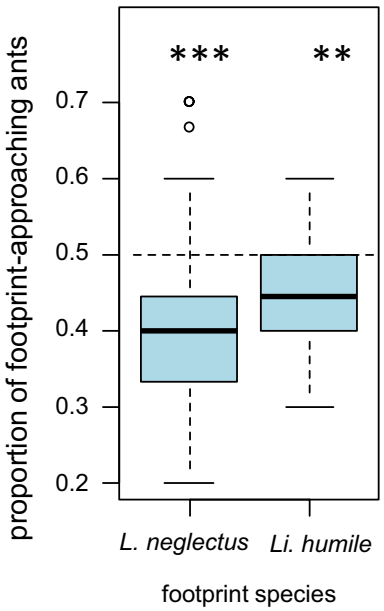


Figure 2. Proportion of footprint-approaching ants (decision ratio) before the experimental treatments. *Lasius niger* tended to avoid footprints of both invasive species. Asterisks indicate difference from random expectation (0.5) (***$p < 0.001$, **$p < 0.01$). Responses to the two footprint species were strongly different ($\chi^2_1 = 15.3$, $p = 9.06 \times 10^{-5}$; Table 1). The figure shows boxplots with median, 1st and 3rd quartiles, range and outliers.

arm, which is 6.6 ± 2.1% less compared to the naïve ants; Supporting information). Neutral encounters resulted in responses which were closer to the random expectation (47.1 ± 1.3% approaching the footprint arm, which is 3.8 ± 1.6% more than the naïve ants). Thus, positive encounters resulted in stronger approaching ($t = 9.04$, $p < 0.0001$), neutral encounters in no significant change albeit a trend to weaker avoidance ($t = 1.78$, $p = 0.078$), and negative encounters in stronger avoidance of footprints of the species the ants had encountered ($t = -3.10$, $p = 0.0024$, Supporting information).

However, the ants did not modify their responses to footprints of the species they had *not* encountered. In the species that *L. niger* workers had not encountered, none of the treatments resulted in a difference to the responses before the confrontations (all $|t| < 1.38$, $p \geq 0.17$; all $df = 128.6$). The effects of *FP = encountered species*, and its interaction with *encounter type* were highly significant (LMER: *FP = encountered_species* $\chi^2_1 = 15.06$, $p = 0.00010$, *encounter type* × '*FP = encountered_species*' $\chi^2_2 = 46.25$, $p < 0.0001$, Fig. 3A, Table 1). Interestingly, although *L. niger* had avoided *L. neglectus* footprints more than those of *Li. humile* before the encounters (effect of *footprint species* in the assays 'before encounters', Table 1), the identity of the species the ants had encountered did not influence the change made by the confrontation (*encounter species* $\chi^2_1 = 0.15$, $p = 0.70$; Table 1). Analysing responses without correcting for the 'naïve' decision ratios yielded similar results (Supporting information).

### Long-term responses

The long-term responses were largely similar to the short-term results. Also here, *L. niger* only responded to footprints of the species they had encountered, but not to footprints of the species they had not encountered (*encounter type* × '*FP = encountered_species*' $\chi^2_2 = 14.02$; $p = 0.00090$, Fig. 3B, Table 1). Positive encounters led to a highly significant preference for footprints of the respective species ($t = 6.69$, $p < 0.0001$, 57.9 ± 1.7%; Supporting information). However, ants with neutral experience did not show responses different from those of naïve ants (47.6 ± 1.6%; Supporting information). As above, the identity of the species the ants had encountered did not affect the change in preference. The only difference between the 1 h and the 48 h assays was that negative encounters did not lead to footprint avoidance any more, even for the species the ants had encountered (42.9 ± 1.7%) (*time* × *encounter type* × *FP=encountered species*: $\chi^2_2 = 6.30$; $p = 0.043$; Supporting information), i.e. *time* was only significant ($t = 2.62$, $p = 0.0093$) for *FP=encountered_species* = TRUE and *encounter type* = *negative* (all other $t < 0.91$, $p > 0.36$). See the Supporting information for detailed percentages of ants approaching the footprint arms.

## Discussion

In this study, we confronted *L. niger* ants with footprints of the invasive *L. neglectus* and *Li. humile*. Naïve ants avoided

Table 1. Statistical results for the proportions of ants choosing the footprint-bearing arm of the Y-maze. The table gives $\chi^2$, df and p values as results of linear mixed-effects models (with interactions), for the assays before the encounters, 1 h and 48 h after the encounters. 'Corrected' means that the proportion of footprint-approaching ants before the encounters (naïve decision ratio) was subtracted from the values after 1 h or after 48 h (respectively) for each worker group. '*FP=encountered_species*' is a variable indicating whether or not footprint species and encountered species are identical. Significant effects are in bold font.

| | Before encounters | | | After 1 h (corrected) | | | After 48 h (corrected) | | |
|---|---|---|---|---|---|---|---|---|---|
| | $\chi^2$ | df | p | $\chi^2$ | df | p | $\chi^2$ | df | p |
| *encounter type* | 0.83 | 2 | 0.66 | 36.83 | 2 | $\mathbf{1.01 \times 10^{-8}}$ | 10.83 | 2 | **0.0044** |
| *FP=encountered_species* | 0.26 | 1 | 0.61 | 15.06 | 1 | **0.00010** | 17.35 | 1 | $\mathbf{3.11 \times 10^{-5}}$ |
| *encountered species* | 0.43 | 1 | 0.51 | 0.15 | 1 | 0.70 | 0.52 | 1 | 0.47 |
| *footprint species* | 15.32 | 1 | $\mathbf{9.06 \times 10^{-5}}$ | 0.02 | 1 | 0.89 | 2.91 | 1 | 0.088 |
| *encounter type* × *FP=encountered_species* | 0.00 | 2 | 1.00 | 46.25 | 2 | $\mathbf{9.06 \times 10^{-11}}$ | 14.02 | 2 | **0.00090** |
| *encounter type* × *encountered species* | 4.45 | 2 | 0.11 | 1.16 | 2 | 0.56 | 1.93 | 2 | 0.38 |
| *encounter type* × *footprint species* | 0.33 | 2 | 0.85 | 1.01 | 2 | 0.60 | 0.72 | 2 | 0.70 |



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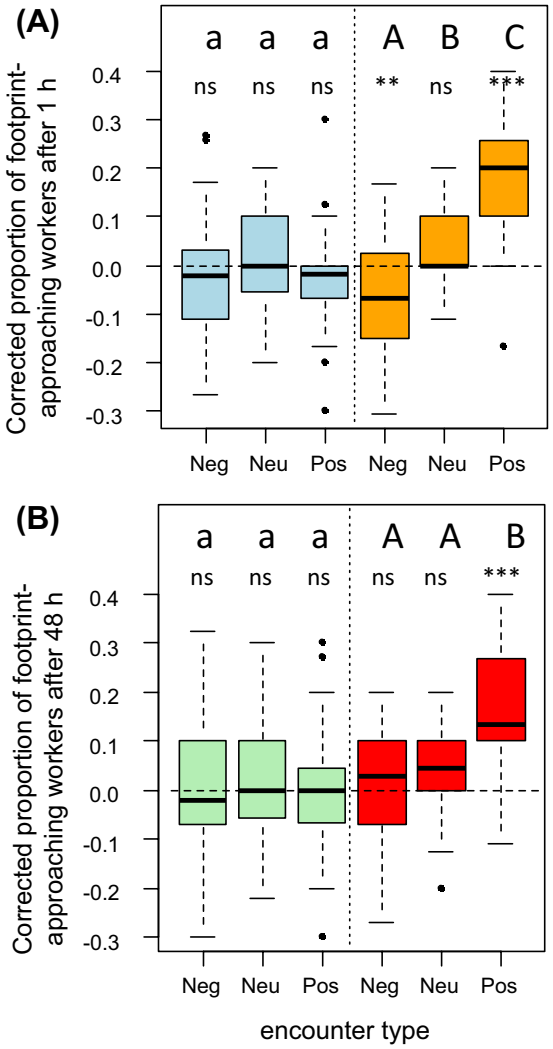


Figure 3. Proportions of footprint-approaching ants (decision ratio) after 1 h (A) and after 48 h (B), corrected for the response of naïve ants (before the encounters). The graphs show the proportion of ants choosing the footprint arm per treatment 1 h or 48 h after the encounters, minus the proportion of ants choosing the footprint arm of the same worker group before the encounters. The treatments are negative (neg), neutral (neu) or positive (pos). Left panels: responses to footprints of the species the ants did not encounter; right panels: responses to footprints of the species which the ants encountered. Asterisks indicate difference from random expectation (zero) (***$p < 0.001$, 'ns' not significant). Plots with same letters within the same panel do not differ significantly from each other according to model summaries. See Table 1 and the Supporting information for statistical details.

footprints of both species. After negative experience, avoidance was stronger compared to the naïve response, whereas after positive experience, workers approached the footprints. Neutral encounters did not result in significant changes compared to naïve responses. Notably, negative or positive experience only affected responses to footprints of the species the ants had encountered, but not those of the other species.

## Ecological benefits of footprint learning

*Lasius niger* ants adaptively adjusted their footprint responses to their experience. They avoided footprints after aggressive encounters, but approached footprints of ants that they had experienced together with food. Notably, this effect was specific to the encountered ant species, but independent of its actual identity, showing that the ants did not generalise but responded specifically to cues of the ant species they had encountered. Such specific responses should be more beneficial than a general neophobia after negative encounters, which would also have been a plausible outcome. Especially the ability to distinguish cues of dangerous predators from those of harmless species, such as herbivores or small predators, should strongly enhance fitness and avoid opportunity costs caused by unnecessary avoidance. The lack of generalisation shown by *L. niger* is highly advantageous, enabling the ants to either avoid superior competitors, or eavesdrop on harmless species that found a food source. In nature, this can be (competitively inferior) ants tending trophobionts or at other food sources, but also aphids themselves, which bear distinguishable cuticular hydrocarbon (CHC) profiles (Lang and Menzel 2011). Hence, ants can learn to discriminate species-specific footprints. Previous studies already showed that ants can discriminate different heterospecific cuticular hydrocarbon (CHC) profiles (Lang and Menzel 2011, Pamminger et al. 2011, Scharf et al. 2011), and habituate to formerly unknown ants (Errard et al. 2006, Menzel et al. 2008a, 2010a). However, to our knowledge discrimination of different footprint profiles was not shown before.

Learned avoidance of other ant species ('anti-competitor behaviour') is comparable to anti-predator behaviour in other systems. The predator cues that induce anti-predator behaviour, but also inducible morphological defenses in prey, are often relatively specific to the predator (Weiss 2019) albeit they can be generalised to congeneric predators (Ferrari et al. 2007). This fits our results for anti-competitor cues. Only few studies suggest innate, strongly generalised anti-predator cues, including visual cues of predators in spiders (Rößler et al. 2022). In our case, generalisation, even to congeneric species, is not possible – the potential competitors belong to the same family (or even to the same genus) as the focal species. CHC profiles are species-specific, but do not allow to infer whether a species might be a superior or inferior competitor, or even the taxonomic clade of the footprint-leaving species (Menzel et al. 2017). Thus, the ants must learn the CHC profile of each competitor. From an evolutionary perspective, learning should be more beneficial than innate responses, since genetic or even epigenetic adaptation to local environments would be too slow to cope with potentially rapidly changing local predator populations. Moreover, innate responses would reduce the success of individuals dispersing to novel environments with unknown predators.

Another novel finding of this study is that the ants successfully associated living or dead ants with their footprints. This is not a matter of course. In a previous study, ants could be positively conditioned to CHCs of another colony in a foraging context, but they kept attacking members of this other



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colony in inter-individual encounters (Bos et al. 2010). Thus, a transfer of experience between foraging context and nestmate recognition context does not always happen. Our setup differs from classical conditioning in that stimuli during the 'training' encounters (living or dead ants) and the 'testing' phase (footprints) were different. Footprints resemble cuticular hydrocarbons but contain less *n*-alkanes (Menzel and Kara unpubl.). Therefore, our experimental setup goes beyond a test of associative learning, as it required ants to transfer information gained from CHCs on entire ants to chemical footprints on paper. In our opinion, it is noteworthy that our ants managed to transfer information between contexts, but also between two similar but not identical chemical mixtures.

### Is competitor naïvete an advantage for invasive species, and is cue similarity relevant?

One presumed advantage of invasive species is 'predator naïvete' or 'prey naïvete' (Sih et al. 2010), that is, native species ignore cues of invasive species, and also fail to learn to respond to them. This can result in lacking anti-predator behaviour against invasive predators. Invasive predators should be especially at an advantage if they are different from any native predator ('novel invaders'), because they elicit weak or no anti-predator behaviour. In contrast, invasive predators that are similar to some native species ('similar invaders') should trigger anti-predator behavior (Sih et al. 2010, Carthey and Banks 2014). Here, 'similarity' concerns the cues invasive and native predators leave in the environment. Cue similarity may be due to phylogenetic relatedness, but not necessarily so if cues evolve rapidly (Menzel et al. 2017). CHCs of *L. neglectus* contain large amounts of alkadienes and methyl-branched alkenes, which are completely absent in the *L. niger* profile (Menzel et al. 2019). In contrast, *Li. humile* possesses mostly monomethyl, dimethyl and trimethyl alkanes, and thus a similar CHC class composition as *L. niger* itself (Buellesbach et al. 2018). Hence, the CHCs of *Li. humile* are more similar to *L. niger* than CHCs of *L. neglectus*, despite higher phylogenetic distance. Still, both cues were learned equally well (no effect of *footprint species* or *encountered species* on the responses after encounters). On a side note, it is notable that the more dissimilar *L. neglectus* cues elicited stronger avoidance by naïve *L. niger* (significant effect of *footprint species* in the assays before encounters, Table 1). We conclude that at least for *Lasius niger*, cue similarity was not relevant for their learning process, although it may influence the naïve responses.

We speculate that learned anti-predator or anti-competitor behaviour may be more common than assumed. For example, learning may explain why anti-predator behaviour is stronger against more common species (Binz et al. 2014a). Predator cues may be learned based on either predator-own cues or cues from the predator's diet, e.g. in faeces (Roberts and Garcia de Leaniz 2011). That ants learned species-specific heterospecific cues also reveals insights to the recognition mechanism itself: it is not only a comparison of the encountered profile with the own profile (Guerrieri et al. 2009, van Zweden and d'Ettorre 2010), but can involve multiple neuronal recognition templates, going beyond a mere distinction of nestmate versus non-nestmate, and also beyond conspecific versus heterospecific. The idea of multiple non-nestmate templates is corroborated by a recent study showing that ants can associate aggressive experiences to certain non-nestmates, and respond more aggressively to colonies after aggressive contact with them (Bey et al. 2025). Thus, discrimination of different non-nestmates seems to become more precise with experience, and may allow a fine-tuned response to non-nestmate individuals as well as their cues.

The specific responses we found contrast to a previous study, where ants were conditioned on single, artificial hydrocarbons and often failed to differentiate between structurally similar hydrocarbons that only differed in chain length (Bos et al. 2012). We suggest that it may be easier for ants to discriminate between entire hydrocarbon blends (such as CHC profiles or footprints) compared to single hydrocarbons (which are rare in nature anyway) because they differ in a higher number of parameters.

### From individual to colony-level behaviour

Our study only dealt with small worker groups. Single individuals can strongly influence foraging behaviour on colony level, and can drive collective decisions in a foraging context (Beckers et al. 1990, Czaczkes et al. 2015). It is possible that in our study, the first ant already influenced the choice of the following ones via its footprints. However this seems less likely because in previous studies, nestmate footprints either had no influence on path choices (Czaczkes et al. 2015) or were avoided (Binz et al. 2014b). In any case, our results indicate that encounters with other ant species can drive path choice of worker groups, be they influenced by the first ant or not. That single foragers influence group-level decisions can be adaptive, because it allows to incorporate individual experiences with other ant species, even if other foragers lack that experience. What is novel here is that individual experience does not only concern the location of food sources, but also the 'meaning' of certain odours which may be associated to food or to danger. Hence, foraging and recruitment is not only influenced by landmarks and footprints (home-range markings) of the own colony (Devigne et al. 2004), but also by the spatial distribution of footprints of other colonies and other species, which forms a blend of home-range markings of multiple species (Popp and Dornhaus 2024) and which is constantly changing due to individual new experiences, but also due to cue decay (Barnes et al. 2002, Narimanov et al. 2024).

Responses after positive encounters were similar after 48 h, suggesting that the information was stored in long-term memory. This coincides with previous studies which showed memories of 24 h in *Lasius* (Czaczkes et al. 2014) or even 72 h in ants and honeybees (Piqueret et al. 2019, Villar et al. 2020). However, it is surprising that the effect of negative experiences was not significant any more after 48h. Usually, animals quickly learn and remember to avoid any threats. Thus, future research is warranted to determine why negative encounters did not result in longer-lasting avoidance.



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## Conclusions and outlook

*Lasius niger* ants can quickly learn to respond to cues of invasive species in an appropriate way. Learned footprint responses can be an important way how ants can reduce competition in a community. Being novel hence might not confer a competitive advantage to invasive ants, at least in respect to competition with native ants. This may be otherwise in taxa such as aphids, which lacked anti-predator responses to cues of an invasive ladybeetle (probably being naïve to this species), but avoided cues of native ladybeetles (Bertleff et al. 2021). We speculate that the ability to learn cue responses may be taxon-specific. It will be interesting to study which taxa can modify cue responses based on experience, and which taxa have innate responses, or no responses at all. Whether the ability to modify cue responses evolved in a taxon might also be linked to the number of its native interaction partners (number of predator, prey or competitor species), but this idea is very speculative.

In our ants, footprint responses depended on individual experience. Therefore, responses are likely to differ between ants from different colonies, but even among nestmates. This suggests that we may not be able to determine species-specific footprint responses, but rather that they are contingent on individual colonies, their health state, size, and other traits. In ants and other arthropods, individual experience hence may result in individual-specific 'landscapes of fear' (Wirsing et al. 2021), and non-consumptive effects caused by predator or competitor cues may be individual-specific as well. Future studies should investigate how footprint responses are linked to a species' or an individual's learning ability, its sensory capacity, but also to animal personality traits like exploration behaviour and boldness (Réale et al. 2007). The interplay of all these traits can determine where individual ants or other arthropods forage (Toscano et al. 2016, Steinhoff et al. 2020, Eccard et al. 2022), and thus drive their exposure to predators and competitors, but also their foraging success.

Finally, we studied learning in native ants here, but it seems plausible that similar abilities may also influence the success of invasive ants themselves. Being able to learn which cues should be avoided or can be exploited may substantially enhance the success of an invading species. Investigating these traits across native and invasive species may hence represent a fruitful research field to advance our understanding of firstly, why some species can cope with novel or invasive species, and secondly, why some species are more successful invaders or colonisers of new habitats than others.

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### Author contributions

**Florian Menzel**: Conceptualization (equal); Formal analysis (equal); Funding acquisition (equal); Methodology (equal); Project administration (lead); Resources (lead); Supervision (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Gülsem Kara**: Data curation (lead); Formal analysis (equal); Investigation (lead); Methodology (equal); Visualization (supporting); Writing – review and editing (supporting).

### Data availability statement

All data are available in the supplement of this article.

### Supporting information

The Supporting information associated with this article is available with the online version.

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