Local coexistence of native and invasive ant species is associated with micro-spatial shifts in foraging activity

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Keywords:
Biological invasions, conservation, Formicidae, impacts, microclimate, shading conditions, *Tapinoma magnum*

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This file is the last version of the manuscript before acceptation for publication in Biological Invasions (www.springer.com/journal/10530).

The published paper can be found here: https://doi.org/10.1007/s10530-021-02678-2

Abstract

Invasive species often displace native species by outcompeting them. Yet, some native species can persist even in heavily invaded areas. The mechanisms mediating this local coexistence are still unclear. Fine-scale microclimatic heterogeneity could promote the local coexistence of native and invasive animal competitors. We tested if native ant species could coexist with a recent ant invader, *Tapinoma magnum*, by shifting their foraging activity in time or space to different microclimatic conditions. We compared the foraging activity of native epigeic ant species among invaded and uninvaded sites. We collected ants at baits in green spaces on the north, east, south and west sides of buildings in the morning, at noon and in the afternoon to test if native species foraged under different microclimatic conditions in invaded sites. Invaded sites had lower ant species richness, diversity, and relative abundance. The native black garden ant *Lasius niger* – one of the most widespread Palearctic ant species – persisted at high densities in invaded areas but foraged less on the east side of buildings and more on the west side. Microclimatic heterogeneity might promote native and invasive species coexistence by allowing some native species to shift their foraging behaviour to locally avoid or outcompete invasive competitors. Better understanding how fine-scale micro-environmental heterogeneity affects native species' persistence in invaded areas could help to predict and locally mitigate the negative impacts of biological invasions.

1 | INTRODUCTION

Invasive species often displace their native competitors (Brown et al. 2002; Kenis et al. 2009; Wong et al. 2021) but some native species succeed in persisting even in heavily invaded areas (e.g., Achury, Holway, & Suarez, 2020; Campbell, Frair, Gibbs, & Rundell, 2015; da Silva Silveira & Guimarães, 2020; Pacioglu et al., 2020). Yet, we know surprisingly little about how native animal species coexist locally with dominant invasive competitors, and in particular whether native species can modify their behaviour to avoid or decrease competition pressure with invaders (Berthon 2015; Ruland and Jeschke 2020).

Fine-scale environmental heterogeneity might promote the local coexistence of native and invasive competitors by allowing native species to shift their foraging or nesting habits towards environmental conditions where they can avoid or outcompete invasive competitors (Melbourne et al. 2007; Nielsen et al. 2010; Hart et al. 2017). Temperature and humidity are crucial components of species' nesting and foraging requirements and are thus expected to affect the local coexistence of competitor species (Albrecht and Gotelli 2001; Žagar et al. 2015; Paterson and Blouin-Demers 2017; Hoffacker et al. 2018). Small scale heterogeneity in thermal conditions are omnipresent in nature because they arise from the shades of geometrical features of the habitat such as terrain slopes, trees and human buildings (Napoli et al. 2016; Pincebourde et al. 2016).

However, the effect of microclimatic heterogeneity on the coexistence of native and invasive animals remains unclear. Existing research has focused mainly on temporal heterogeneity such as seasonal or daily variations in temperature (Holway 1998; Roeder et al. 2018), but it is still unknow if, at a local scale (i.e., within habitats), spatial heterogeneity in microclimatic conditions can promote the coexistence of native and invasive competitors.

To address this question, we studied the effects of temporal and spatial microclimatic heterogeneity on the foraging activity of native and invasive ant competitors. Ants are an ideal model system to study the ecological effects of microclimatic conditions because they are small ectotherms whose nesting and foraging patterns are strongly influenced by variations in temperature (Spicer et al. 2017; Roeder et al. 2018). In addition, ants occupy every terrestrial landmass on Earth except Antarctica and thrive in human-altered environments such as urban and suburban areas (Pećarević et al. 2010). Urban ant communities do not strongly differ from adjacent non-urban communities but often comprise invasive species because human-mediated introduction events are more likely in urbanized areas (Perez and Diamond 2019; Dáttilo and MacGregor-Fors 2021). Moreover, urbanized areas are characterized by disturbed habitats that often favour invaders over native species (Holway et al. 2002b; Cadotte et al. 2017).

Invasive ants are among the fastest spreading and the most damaging animals worldwide (Rabitsch 2011). Most invasive ant species are behaviourally dominant competitors that form large colonies (sometimes called ‘supercolonies’) that can cover several hectares and are composed of hundreds to thousands of interconnected nests hosting thousands of queens and millions of workers (Holway et al. 2002a). Areas invaded by invasive ants are generally characterized by low native species richness and abundance compared to adjacent non-invaded areas (e.g., up to 90% decrease in abundance in areas invaded by the Red Imported Fire Ant (*Solenopsis invicta*); Porter & Savignano, 1990; Wittman, 2014). Yet, native ant species frequently persist in areas heavily invaded by invasive ant species (Tartally 2006; Guénard and Dunn 2010; Vonshak et al. 2010; Wittman 2014). Understanding how microclimatic heterogeneity affects ant invasions is thus a conservation priority because it could help to limit the spread of invasive species and mitigate their impacts on native communities.

We used the shades generated by buildings as a source of temporal and spatial microclimatic heterogeneity. Variations in shading conditions are omnipresent in terrestrial environments. As surface temperature increases with the amount of absorbed solar radiation, shades can generate important microclimatic variations in space and time (Napoli et al. 2016; Pincebourde et al. 2016). To test if temporal and spatial microclimatic heterogeneity generated by buildings promote the coexistence of native and invasive ant species at local scale, we baited ants around residential buildings (on north, east, south and west sides) in the morning, at noon and in the afternoon (because shades' position changes along the day) in the presence or absence of a dominant invasive competitor: *Tapinoma magnum*.

Tapinoma magnum, probably native from northern Africa, is an emergent invasive species of great ecological and economic concern in Europe because it can easily establish and thrive in all Europe (Dekoninck et al. 2015; Janicki et al. 2016; Seifert et al. 2017), in contrast to most other invasive ants that are limited to the Mediterranean area. The species is probably transported with plant material (it was found in garden centres and tree nurseries; Dekoninck et al., 2015; Seifert et al., 2017) and several well-established populations are known in Belgium, France, Germany and Switzerland (Seifert et al. 2017; Bujan et al. 2021). The impacts of *T. magnum* on native biodiversity are still unknown but its dominant behaviour and supercolonial social structure (i.e., individuals mix freely within large supercolonies containing a high number of interconnected nests) suggest that the species is highly detrimental to native ant communities (Dekoninck et al. 2015; Warren et al. 2019).

In this study, we first tested the impact of *T. magnum*'s invasion on the richness, diversity, relative abundance and composition of native epigeic ant communities and identified which species were able to coexist with *T. magnum*. Then, we tested if native ants that persisted in invaded areas changed their temporal foraging patterns or spatial location compared to non-invaded areas.

2 | MATERIALS AND METHODS

2.1 | Study sites

Our study area is a residential area of the municipality of St-Sulpice, Switzerland (WGS84 coordinates: 46.51329, 6.55624). This area is partially invaded by a large colony of *Tapinoma magnum*, covering at least four hectares. The species was detected in this area for the first time in 2012 but it is likely that it was introduced even earlier (D. Cherix, *Pers. Comm.*). In July 2019, we sampled ants at eight invaded and eight non-invaded sites. All sampling sites were in a homogenous environment composed of green spaces surrounding houses and buildings that are very similar in vegetation type and management intensity (i.e., short lawns with some bushes and trees). Each sampling site corresponded to a green space surrounding a residential building (buildings were constructed between 1974 and 2015; mean ± SD: 1993 ± 14) (Fig. 1a, b). We selected only large buildings (i.e. shortest side longer than 12 meters) surrounded by green spaces and with four sides accessible. For each site, sampling permission was obtained from the inhabitants of the building. Vegetation richness and height, dominant ground species, as well as the presence of bushes or trees were recorded for each sampling site. However, as these variables were consistent across sites, they were not included in the statistical analyses. Ground temperature has been linked to foraging intensity in ants (e.g., Azcárate et al. 2007). Thus, to verify that the time of the day and the side of building affected ground temperature we measured it using a thermometer probe (IHM multi-use digital stem thermometer 2263AT), during each sampling event and for each side of the building (at the most central point of the sampling area; see Fig. 1b).

2.2 | Ant sampling

Because shades follow the position of the sun during the day, each sampling site was sampled at three different times of the day: in the morning (between 7h00 and 10h30), at noon (between 12h00 and 15h30) and in the afternoon (between 16h30 and 20h00). For a given site, each of the three sampling events (morning, noon and afternoon) was conducted on a different day (Supplementary Data) to avoid that foraging trails created in the morning affect ants' foraging behaviour at noon and in the afternoon (Jackson et al. 2006). In addition, as it was not possible to sample several sites simultaneously (the sampling was performed by one person), this sampling design allowed to prevent a potential confounding effect between the day of sampling and the sampling site. Thus, a total of 48 sampling events were performed (16 sampling sites sampled three times; Fig. 1a). Each sampling event consisted of depositing 40 baits in the green space surrounding the building. The baits (1,920 baits in total) were Eppendorf tubes (2mL) one-third filled with cotton impregnated with food. Since ant species can have different food preferences (Csata and Dussutour 2019), two types of Eppendorf tubes were prepared: 1,920 Eppendorf tubes were impregnated with honey (15% honey and 85% water solution) and another 1,920 Eppendorf tubes were impregnated with tuna (50% canned tuna and 50% water solution). Thus, one bait corresponds to a pair of tubes. To record spatial variations in ants foraging activity, the 40 baits were evenly placed at each side of the building (10 to the north, 10 to the east, 10 to the south and 10 to the west; Fig. S1) in two transects of five baits (Fig. 1b). The first transect was one meter away from the building wall, whereas the second transect was four meters away from the first transect. On each transect, baits were placed every four meters. The exact position of baits could sometimes slightly differ from the ideal setup because of the presence of paved or partially inaccessible areas (building entry, parking lot). In these situations, baits were placed as close as possible from the ideal position, while keeping at least four meters between them (Fig. S1). Baits were placed around the buildings in a consistent way across all three sampling events. They were placed on the ground and left open for one hour, after which they were rapidly closed and collected in the same order in which they were deposited. Finally, baits were stored at -20°C until species identification. All ants were counted and identified to either species or genus level using Seifert's (2007) ant identification key and then stored at -20°C in 90% ethanol for long term conservation. Ants from the genus *Temnothorax* and *Tetramorium* were not identified to the species level because their morphological identification is not reliable (only two workers of *Temnothorax* were sampled, which is not enough to perform a proper identification in this genus, and *Tetramorium* species need to be identify with genetic markers or complex morphometrics; Wagner et al. 2017). Bait sampling is a common method to sample epigeic ants (i.e., ants foraging above ground) and is a classic tool to study competition between ant species as well as invasive ants' impacts on native ant communities (Porter and Savignano 1990; Bestelmeyer et al. 2000; Albrecht and Gotelli 2001; Thomas and Holway 2005; Roeder et al. 2018). However, this sampling method might not be suitable to detect and estimate the foraging activity of subterranean ant species (e.g., *Lasius flavus*) because they forage mostly underground. Finally, as ants can forage several meters away from their nest, this sampling design (i.e., baits every four meters) cannot differentiate between one colony foraging on several baits or multiple colonies foraging on one bait each.

2.3 | Microclimatic variations induced by shading conditions

To control that ground temperature was linked to the time of the day (i.e., morning, noon and afternoon) and the side of the building (i.e., north, east, south and west), and that it did not differ among invaded and non-invaded sites, we used a Gaussian generalized mixed-effect model (R package 'glmmTMB'; Brooks et al. 2017) with ground temperature (in °C) as the response variable and time of the day (morning, noon and afternoon), building side (north, east, south and west), zone (invaded and non-invaded) and their interactions as fixed effects, and sampling site and date as random effects (N = 192 measurements; Fig. 1c, d). We used analyses of deviance (i.e., Type III Wald χ^2 tests) to assess which variables and interactions had significant effects on each response variables. Ground temperature was best explained by the interactive effect of time of the day and building side (N = 192, $R^2_{conditional}$ = 0.71, $R^2_{marginal}$ = 0.53; see Fig. 1d).

2.4 | Effect of *T. magnum* on native ant communities

We tested if the presence of *T. magnum* affected native ant species' richness, diversity and relative abundance, as well as their community composition. Native species richness was calculated as the number of native species, native species diversity as the Shannon diversity index (R package 'vegan'; Oksanen et al. 2020) and native species relative abundance as the proportion of baits occupied by native ant species by sampling events (N = 48 sampling events). We compared the richness, diversity and relative abundance of native ant species between invaded and non-invaded sites using generalized linear mixed models (with Gaussian link functions for richness and diversity and Binomial link function for relative abundance) with sampling site and date as random effects observations (R package 'glmmTMB'). We visualized if the composition of native ant communities differed among invaded and non-invaded sites using Nonmetric Multidimensional Scaling (NMDS; R package 'vegan'). We also assessed differences in community composition among building side (north, east, south and west) and time of day (morning, noon, afternoon) NMDS simplifies multivariate data into a few important axes, allowing to better assess differences among groups. We computed the NMDS using the number of baits occupied by each species on each building side at each sampling event (N = 192). We tested the differences in community composition between groups (invaded/non-invaded, north/east/south/west and morning/noon/afternoon) using permutational multivariate analyses of variance (PERMANOVA; R package 'vegan').

2.5 | Effects of *T. magnum* on native ants' foraging activity in time and space

We measured the foraging activity of native and invasive ant species as the proportion of baits that they occupied at each building side (north, east, south, west) at each sampling event (*N* = 192 building sides, 48 sampling events, 16 sampling sites; Fig. 1). We tested the interactive effects of *T. magnum*'s presence, time of the day and building side on foraging activity in the four most frequent native ant species: *Lasius niger*, *Myrmica specioides*, *Myrmica sabuleti* and *Tetramorium* sp. These species occupied more than five percent of the baits in non-invaded sites (31% for *L. niger*, 10% for *M. specioides*, 8% for *M. sabuleti* and 6% for *Tetramorium* sp.; Fig. 3). We also tested the effect of time of the day and building side on the foraging activity of *T. magnum* (*N* = 96 building side, 24 sampling events, 8 sampling sites; Fig. 1a). We used Binomial linear mixed models (R package 'glmmTMB') to test the effects of invasion (invaded or non-invaded sites), time of the day (morning, noon or afternoon), building side (north, east, south or west) and all possible first-degree interactions on the proportion of baits occupied at each building side (10 baits were placed at each building side per sampling event). The sampling site and date were set as random effects to account for spatial and temporal dependency of observations(Brooks et al. 2017). For each model, we used a backward selection procedure to determine the best fitting model by sequentially removing non-significant fixed effects using type III Wald χ^2 tests (R package 'car'; Fox & Weisberg, 2019). We controlled for the validity of the best-fitting models by analysing models' residuals (R package 'DHARMa'; Hartig 2018). Models' estimations and *post hoc* comparisons (with Tukey corrections) were computed using the R package 'emmeans' (Lenth 2020). Models' performance was assessed by computing pseudo-R^2 using the R package 'performance' (Ludecke et al. 2019). All statistical analyses were performed in R 4.0.3 (R core team 2020).

3 | RESULTS

3.1 | Effect of *T. magnum* on native ant communities

We recorded 15 species from eight genera during this study (Fig. 3), which represents ~20% of species occurring at regional scale (i.e., in the Vaud canton; www.fourmisvaud.ch) and ~10% of species occurring in Switzerland (www.antmaps.org). *T. magnum* was the only non-native species detected. At non-invaded sites, *Lasius niger* was the most abundant species (mean ± s.e. = 31 ± 5% of baits occupied), followed by *Myrmica specioides* (10 ± 2%), *Myrmica sabuleti* (8 ± 3%) and *Tetramorium* sp. (6 ± 4%); other species occurred in <5% of baits (Fig. 3). In invaded sites, *T. magnum* was the most abundant species (35 ± 7%), followed by the *Lasius niger* (30 ± 2%), *Myrmica specioides* (4 ± 1%) and *Tetramorium* sp (2 ± 1%) (other species occurred in ≤1% of baits; Fig. 3). The presence of *T. magnum* was associated with lower richness (χ^2 = 11.1, *df* = 1, *P* < 0.001; Fig. 2a), relative abundance (χ^2 = 35, *df* = 1, *P* < 0.0001; Fig. 2b) and diversity (χ^2 = 7.8, *df* = 1, *P* = 0.005; Fig. 2c) of native ant species. Yet, the total ant relative abundance differs only marginally between non-invaded and invaded sites (χ^2 = 3.5, *df* = 1, *P* = 0.06; Fig. 3). The proportion of baits occupied by *M. specioides* and *M. sabuleti* was lower in invaded than in non-invaded sites (For *M. specioides,* χ^2 = 4.7, *df* = 1, *P* = 0.03; For *M. sabuleti*., χ^2 = 7.5, *df* = 1, *P* = 0.006; Fig. 3). However, the proportion of baits occupied by *L. niger* and *Tetramorium* sp. did not differ between invaded and non-invaded sites (For *L. niger*, χ^2 = 0.6, *df* = 1, *P* = 0.45; For *Tetramorium* sp., χ^2 = 1.3, *df* = 1, *P* = 0.25; Fig. 3). The composition of native ant communities was affected by *T. magnum*'s invasion (*F* = 6.5, R^2 = 0.03, *P* = 0.001) and by the time of the day (*F* = 6.9, R^2 = 0.07, *P* = 0.001) but not by the side of the building (*F* = 1.03, R^2 = 0.02, *P* = 0.4). However, the differences in community composition between invaded and non-invaded sites as well as between morning, noon and afternoon sampling were relatively small (Fig. 4).

3.2 | Effects of *T. magnum* on native ants' foraging activity in time and space

The proportion of baits occupied by native species was affected by the time of the day in *M. specioides* ($\chi^2 = 29.5$, $df = 2$, $P < 0.0001$) and *M. sabuleti* ($\chi^2 = 12$, $df = 2$, $P = 0.002$) and by building side in *M. sabuleti* ($\chi^2 = 16.8$, $df = 3$, $P = 0.0008$), *Tetramorium* sp. ($\chi^2 = 14.6$, $df = 3$, $P = 0.002$; Table 1). Invasion and building side had an interactive effect on the probability of foraging on baits in *L. niger* ($\chi^2 = 13.5$, $df = 3$, $P = 0.004$; Table 1). *Lasius niger* was not affected by invasion on the north and south sides of buildings (*odds ratio* = 0.63 and -0.36 respectively, $df = 180$, $P > 0.05$), but it was foraging less on the east side (*odds ratio* = 1.9, $df = 180$, $P = 0.06$), and more on the west side of buildings (*odds ratio* = -2, $df = 180$, $P = 0.04$; Fig. 5) in invaded sites compared to non-invaded sites.

4 | DISCUSSION

Our field study demonstrated that *Tapinoma magnum* had a negative impact on native epigeic ant communities and should therefore be considered an important ecological threat for Europe and other temperate regions worldwide. We found that *Lasius niger,* the most abundant native ant in our study area, persisted in sites invaded by *T. magnum* and shifted its foraging activity spatially towards the west side of buildings compared to non-invaded sites where it was more active on the east side (Fig. 5). This suggests that west-exposed green spaces benefited *L. niger* by allowing the species to either avoid or outcompete *T. magnum* while the east-exposed green spaces would have the opposite effect. However, it is not clear why west-exposed green spaces favoured *L. niger* over *T. magnum* as they did not strongly differ in ground temperature from other building sides, contrarily to north-exposed areas that were up to 6°C cooler than other sides (Fig. 1d).

Our findings suggest that microclimatic heterogeneity promotes the persistence of *L. niger* in areas invaded by its invasive competitor *T. magnum*. *Lasius niger* is among the most widespread native species in the Palearctic realm (www.antmaps.org) and is notoriously abundant in open-vegetated habitats from urban cores to semi-natural areas (Gippet et al. 2017). Thus, *L. niger* is probably the most frequent native competitor for invasive ants in European landscapes and might be able to limit the spread of invasive ant species either by monopolizing available resources or physically dominating the invader. Our results are consistent with previous findings that invasive ants (*Lasius neglectus*) can be outcompeted by native competitors under certain environmental conditions (i.e., > 30°C; Frizzi et al. 2017) and that *L. niger* is a challenging competitor that can limit the foraging success of highly invasive species such as Argentine ants (*Linepithema humile* ; Cordonnier, Blight, Angulo, & Courchamp, 2020). However, it is possible that, over time, *T. magnum* can displace *L. niger* from baits (Thomas and Holway 2005; Carval et al. 2016). This is beyond the scope of our study which focused the ant's immediate foraging response by collecting ants one hour after placing the baits in the field. It is also unclear if the presence of *T. magnum* alters the spatial distribution of *L. niger*'s colonies (i.e., fewer colonies of *L.niger* on the east-exposed green spaces), or if *L. niger* colonies maintained their pre-invasion spatial distribution but changed their foraging strategy to better avoid or outcompete *T. magnum* (e.g., changes in the foraging distance or number of foragers recruited). Phenotypic plasticity in thermal tolerance, competitive behaviour or diet (Bujan et al. 2020; Balzani et al. 2021; Trigos-Peral et al. 2021) might help species co-exist locally, for example by limiting direct competitive interactions. Future research could explore if it enables *L. niger* to persist in invaded areas.

In other native ant species (*M. specioides* and *M. sabuleti*), foraging activity uniformly decreased in invaded sites (Fig. 3, Table 1) and did not shift towards different time of day or building side (Table 1). This suggests that not all native species can modify the microclimatic conditions at which they forage in response to invasion, either because their plastic response is limited (e.g., great territoriality, limited foraging distance from nests) or because, in invaded sites, the two most dominant species – *T. magnum* and *L. niger* – already occupied most available resources (Savolainen and Vepsäläinen 1988). Behavioural shifts of native species (i.e., foraging or nesting) induced by the presence of an invasive competitor were observed in various native animals including fish, amphibians, reptiles, insects and molluscs (Thomson 2004; Alcaraz et al. 2008; Wright et al. 2010; Stuart et al. 2014; da Silva Silveira and Guimarães 2020) and it would therefore be interesting to assess to which extent the availability of alternative microenvironmental conditions help species to behaviourally respond to invaders or to find micro-refuges (Astorg et al. 2020).

Overall, native ant communities were poorer in invaded areas. However, our sampling method cannot evaluate *T. magnum*'s impacts on subterranean ant communities because it detects only ground-foraging species. Yet, it is likely that *T. magnum* might have little or no impacts on subterranean ant species (eg, *Lasius flavus*) because they occupy a different ecological niche (Holway et al. 2002a). It also possible that we missed species that are present in the area because we collected baits after one hour. Future studies could thus combine several sampling methods (eg, baits and pitfall traps; Porter and Savignano 1990) or more intense baiting design (eg, bait collection every hour over a 24 hours period; Albrecht and Gotelli 2001) to get a more complete picture of native ant communities in invaded and non-invaded sites. Our results show that *T. magnum* impacts native epigeic ant communities and suggest that the spread of this new invasive ant species might threaten other ground-dwelling arthropod taxa, as is the case with the invasion of *Lasius neglectus*, another highly invasive ant in Europe (Nagy et al. 2009).

To date, ~40 ant species have established invasive populations in Europe (Rabitsch 2011; Schifani 2019), yet, only *Lasius neglectus* and *Tapinoma magnum* (and to a lesser extent

Linepithema humile), can grow large outdoor super-colonies in central and northern Europe, while other invasive ant species are limited to the Mediterranean area (Ugelvig et al. 2008; Charrier et al. 2020). Thus, the spread of *T. magnum* threatens all Europe and it is likely that the species can established in other parts of the world if introduced by human activities such as the global horticultural trade (Dekoninck et al. 2015; Seifert et al. 2017). Eradicating established invasive populations is costly, often fails and does not prevent reintroduction events (Pluess et al. 2012; Ujiyama and Tsuji 2018). Thus, it is urgent to manage this new invasion by preventing human-mediated dispersal of *T. magnum* to new locations (Gippet et al. 2019) and by limiting its impacts where it is already established (e.g., Guyot et al. 2015). Understanding how microclimatic conditions shape native and invasive species foraging activities offers promising insights to efficiently combat biological invasions. Taking advantage of microclimatic conditions might help design more target-specific eradication campaigns (Buczkowski et al. 2018) by, for example, depositing poisoned baits at the precise location and time that maximizes poison intakes by the invader and minimizes it for its native congeners. Finally, rather than trying to eradicate established invasive populations, it might sometimes be more efficient to mitigate their negative impacts by helping native species to locally outcompete them (Guo et al. 2018). In habitats that are particularly threatened by invasive species introductions (e.g., urban green spaces, residential areas), increasing microclimatic and more generally environmental heterogeneity may be an effective, environmentally friendly, cheap, and easy way to limit the impacts of invasive species. Homogenous habitats (e.g., lawns) could be avoided by creating microenvironmental heterogeneity in shading conditions (e.g., by planting trees or building artificial terrain slopes) but also in soil properties (e.g., type, compaction), vegetation management (i.e., heterogenous mowing; e.g., Suggitt et al. 2011) and in irrigation practices (i.e., heterogenous watering).

Our results highlight the potential role of micro-environmental heterogeneity in mediating native and invasive species coexistence. However, additional research is needed to generalize our findings and to address the mechanisms involved. Our study was performed in a single suburban area composed of very homogenous and highly maintained lawns. Replicating our experiment in other landscape contexts and seasons would thus allow to better assess the consistency of our findings across different urban areas as well as its validity in rural and semi-natural habitats (e.g., pastures, meadows, scrublands). However, to replicate our experiment in other locations, adjacent invaded and non-invaded areas composed of similar non-homogenous habitats are required (e.g., Angulo et al. 2011). If this set-up is not possible, researchers may test the effects of micro-environmental heterogeneity on native and invasive ants' coexistence by experimentally adding shaded microhabitats to adjacent invaded/non-invaded environments (e.g., Wittman et al. 2010). This would allow generating microclimatic heterogeneity independently of the time of the day and to avoid the constraints linked to the utilization of buildings to generate shade as building walls are not always perfectly aligned with the cardinal directions. Yet, despite these limitations understanding the micro-environmental consequences of human buildings is interesting because invasive species often thrive in urbanized areas.

5 | CONCLUSION

Shades are an omnipresent source of spatial and temporal microclimatic heterogeneity. Yet, their consequences on species' foraging activity, community structure and their potential role in the local coexistence of native and invasive species are understudied (Stahlschmidt and Johnson 2018; Ibarra-isassi et al. 2021). This study is a first step towards understanding how shading conditions could mediate the local coexistence of native and invasive competitors and should stimulate future research to explore the effects of fine-scale environmental heterogeneity on native and invasive species coexistence and how these effects might change across seasons or at other latitudes.

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Acknowledgements

This work was funded by the Swiss Canton Vaud, the Fond National Suisse, and the Programme de la Famille Sandoz—Monique de Meuron pour la relève universitaire. We thank J. Bujan and G. Fenn-Moltu and two anonymous reviewers for helpful comments on an earlier version of the manuscript.

Declarations

Funding

This work was funded by the Swiss Canton Vaud, the Fond National Suisse, and the Programme de la Famille Sandoz—Monique de Meuron pour la relève universitaire.

Conflicts of interest

The authors declare no conflicts of interest.

Availability of data and material

The data that support the findings of this study are openly available at https://github.com/JGippet/Tmagnum_impacts.

Code availability

The R code and data used to perform statistical analyses and associated figures are openly available at https://github.com/JGippet/Tmagnum_impacts.

Authors' contributions

J.M.W.G. and C.B. designed the study. L.G. carried out field sampling. L.G. and J.M.W.G. identified the ants. J.M.W.G. and L.G. carried out data processing and statistical analyses. All authors wrote the manuscript.

Ethics approval

No ethic approval was needed

Consent to participate

Not applicable

Consent for publication

Not applicable

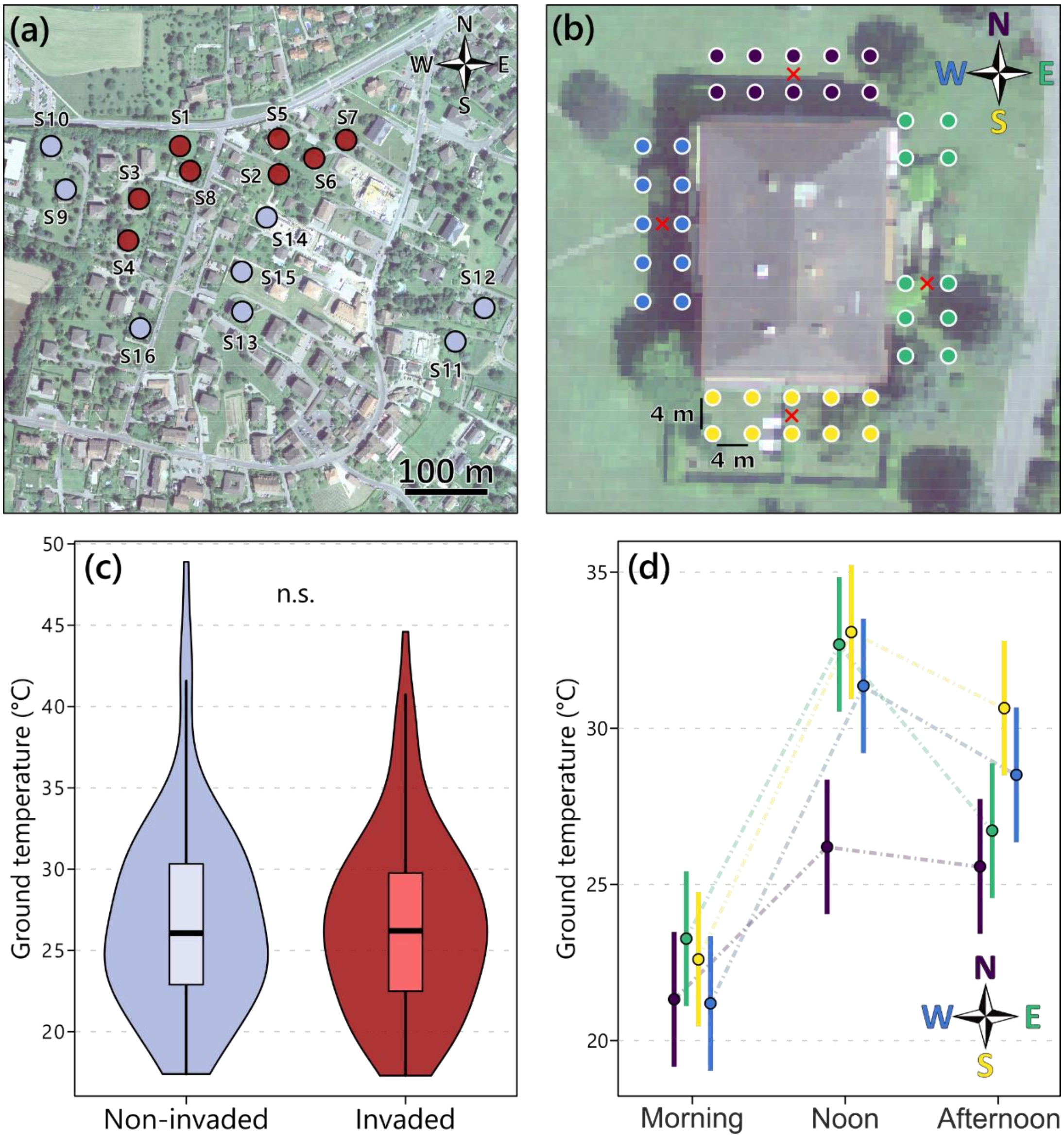

Fig. 1. Sampling design. **(a)** Position of the eight invaded (dark-red dots) and the eight non-invaded (light blue dots) sampling sites; **(b)** A typical sampling site composed of a green space surrounding a building. Baits (colored dots) were placed in a standardized way around the buildings. The red crosses indicate where ground temperature was measured for each sampling event; **(c)** Average ground temperature in invaded and non-invaded sampling sites; **(d)** Estimation of ground temperature depending on time and building side (according to the best fitting model: Temperature ~ Time * Side; marginal $R^2 = 0.53$).

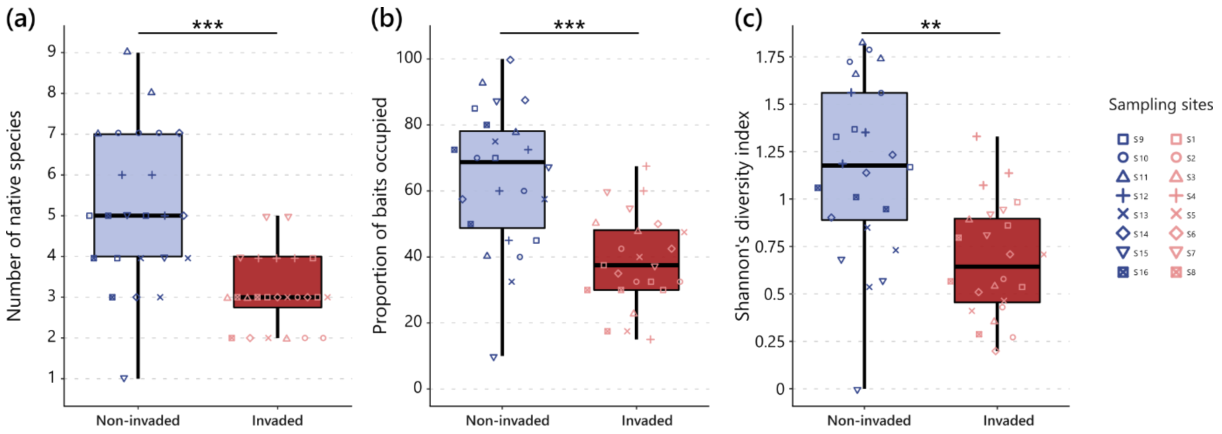

Fig. 2. Impact of *Tapinoma magnum* on **(a)** the richness, **(b)** the relative abundance and **(c)** the diversity of native ant species. Coloured boxes contain 50% of the data (the median is the central thick horizontal line) and whiskers contain the lowest and highest 25% of the data. Data points are represented as symbols (horizontally jittered for visual purpose). For comparisons between groups, **: P < 0.01, ***: P < 0.001.

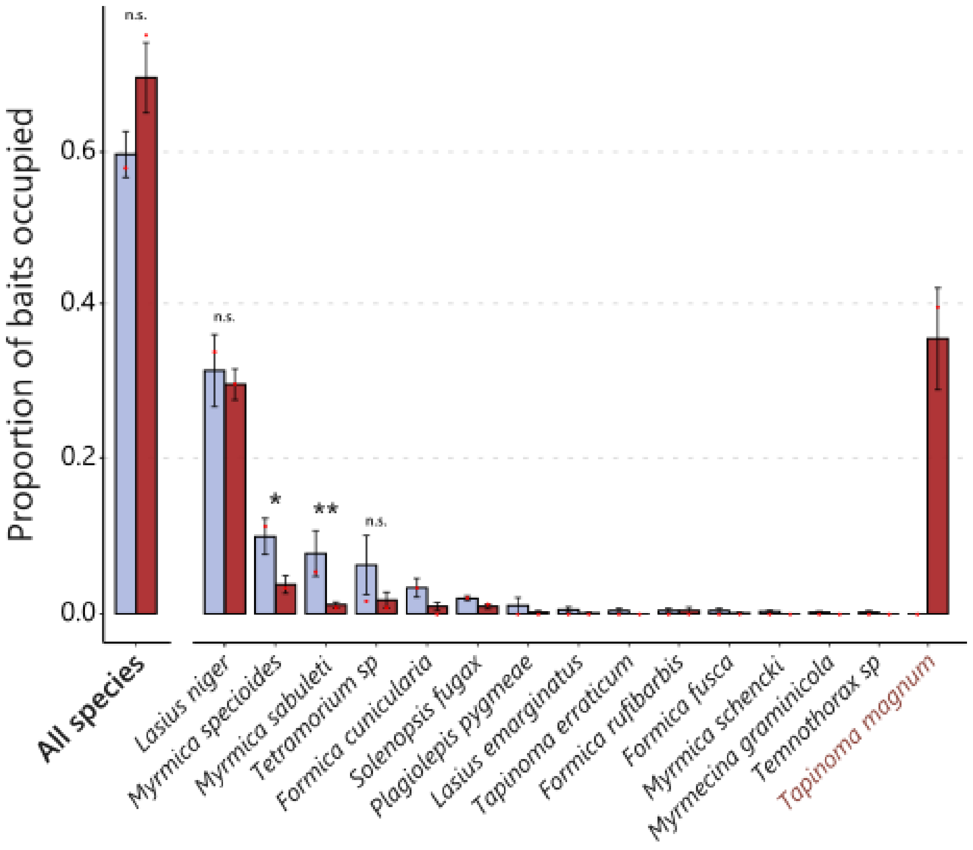

Fig. 3. Coloured bars represent the mean proportion of baits occupied by ants in invaded (*N* = 8; dark red) and non-invaded (*N* = 8; light blue) sites. Error bars represent standard errors around the mean and red dots are median values for each group. For comparisons between groups, n.s.: non-significant, *: P < 0.05, **: P < 0.01.

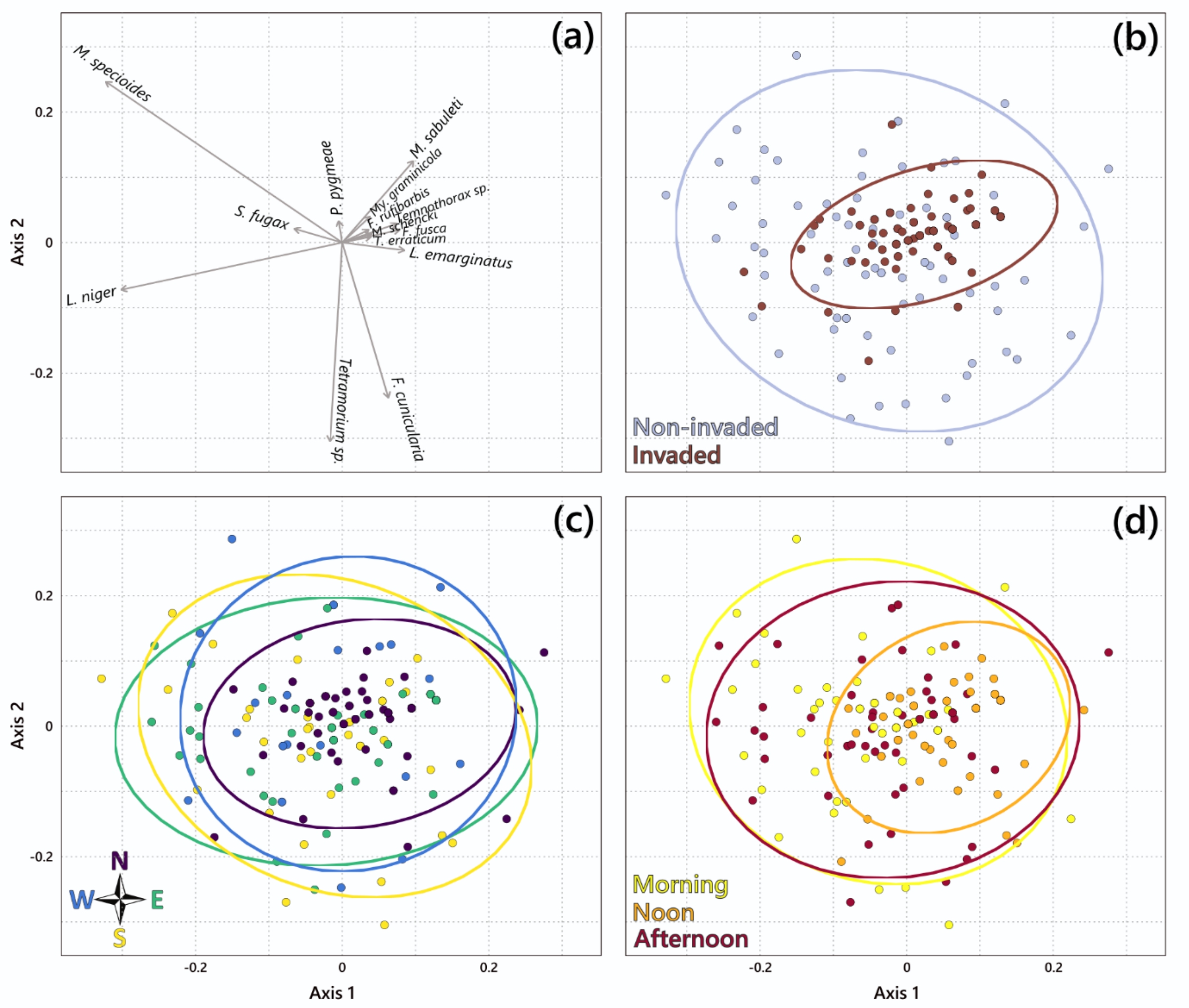

Fig. 4. Composition of native ant communities. **(a)** Arrows represent the contribution of each species on each axis of a non-metric multidimensional scaling (NMDS) biplot. **(b, c, d)** Dots (*N* = 192) represent the ant communities at each side of building and time of the day for each sampling site (16 sampling sites * 3 times * 4 sides). Dots were coloured to assess the difference in ants' community composition between **(b)** invaded and non-invaded sites, **(c)** side of building (North, East, South, West) and **(d)** time of day (morning, noon, afternoon). Ellipses include 95% of the dots of each group.

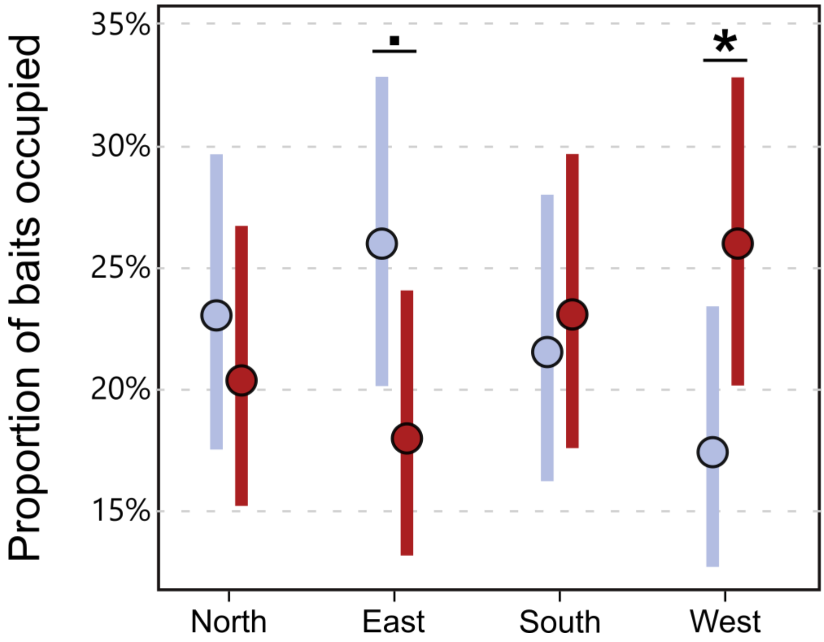

Fig. 5. The effects of *Tapinoma magnum*'s invasion (invaded sites in red and non-invaded sites in blue) on the proportion of baits occupied by the native ant *L. niger* depends on the side of the building. Dots and bars are mean ± 95% CI estimations of the best-fitting model (Table 1). Asterisks indicate significant differences between invaded and non-invaded sites (·: $P < 0.1$, *: $P < 0.05$).

Table 1. Effects of *T. magnum*'s invasion (i.e., invaded vs non-invaded), time of the day (morning, noon, afternoon) and exposition (north, east, south, west) on the proportion of baits occupied, at each building sides, by *Lasius niger*, *Myrmica specioides*, *Myrmica sabuleti*, *Tetramorium* sp. (N = 192 building sides) and *Tapinoma magnum* (only in invaded sites; N = 96 building sides). Ten baits were deposited at each building side during each sampling events (Fig. 1, Fig. S1). Dark blue cells indicate significant effects ($p < 0.05$). Models' statistical details are in Table S1.

	Probability of baits occupied						
	Invasion	Time	Building side	**Invasion : Time**	**Invasion : Building side**	Time : Building side	**Pseudo-R^2** (fixed effects only)
Tapinoma magnum	▨			▨	▨		0.01(0)
Lasius niger	■	■	■		■		0.03 (0.027)
Myrmica specioides	■	■					0.21(0.2)
Myrmica sabuleti	■	■	■				0.29 (0.27)
Tetramorium sp.			■				0.18 (0.12)

Table S1. Analyses of deviance (Type III Wald χ^2 tests) of the best fitting models of the proportion of baits occupied (Binomial GLMs) by each native ant species (N = 192 building sides and 16 sampling sites) and *T. magnum* (N = 96 building sides and 8 sampling sites) (See Table 1).

Proportion of occupied baits (Binomial model)	**Species**	**Best model**	χ^2	**df**	***P***
	Lasius niger	(Intercept)	28.87	1	< 0.0001
		Invasion	0.4	1	0.53
		Building side	7.04	3	0.07
		Time of day	22.23	2	< 0.0001
		Invasion : Building side	13.45	3	0.004
	Myrmica specioides	(Intercept)	43.05	1	< 0.0001
		Invasion	4.79	1	0.03
		Time of day	29.5	2	< 0.0001
	Myrmica sabuleti	(Intercept)	39.07	1	< 0.0001
		Invasion	7.66	1	0.006
		Building side	16.84	3	0.0008
		Time of day	12.03	2	0.002
	Tetramorium sp.	(Intercept)	73.3	1	< 0.0001
		Building side	14.58	3	0.002
	Tapinoma magnum	(Intercept)	21.86	1	< 0.0001

Fig. S1. Position of the baits around each sampling sites. Large dots indicate building used as invaded (red) and non-invaded (blue) sampling sites. Small dots give the approximate (±1 m) position of baits around the buildings. Their colour indicates the cardinal category at which they were assigned. Background satellite view is from Esri, Digital Globe, Earthstar Geographics.