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Impact of temperature and season on ant foraging activity of two invasive species in a Mediterranean urban area

Giovanny Destour¹  | Rumsais Blatrix¹  | Aurélien Caries¹  |
 Juliette Genevet¹  | Bernard Kaufmann²  | Baptiste Lecoq¹  | Annick Lucas¹  |
 Killian Verlingue¹  | Alan Vergnes³  | Marion Javal^{1,4} 

¹CEFE, Université de Montpellier, CNRS, EPHE, IRD, Montpellier, France

²Université Claude Bernard Lyon 1, LEHNA UMR 5023, CNRS, ENTPE, Villeurbanne, France

³CEFE, Université Paul Valéry Montpellier 3, Université de Montpellier, CNRS, EPHE, IRD, Montpellier, France

⁴CBGP, IRD, CIRAD, INRAE, Institut Agro Montpellier, Université de Montpellier, Montpellier, France

Correspondence

Marion Javal, CEFE, Université de Montpellier, CNRS, EPHE, IRD, 34293 Montpellier, France.
 Email: marion.javal@ird.fr

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Abstract

1. Invasive species often have harmful effects on human activities and biodiversity. The *Tapinoma nigerrimum* complex includes three species that exhibit invasive traits and the ability to form supercolonies, including *Tapinoma magnum* and *Tapinoma darioi*. While these species are native to the Mediterranean basin, they have recently been reported as invasive in more northern regions of Europe. However, *T. magnum* and *T. darioi* show different invasion patterns in Europe, suggesting differences in thermal preferences between these species. We aimed to determine whether there was any difference in activity pattern depending on temperature or season between the two *Tapinoma* species and between *Tapinoma* and co-occurring native Mediterranean ants.
2. We measured ambient temperature and ant foraging activity around the nest entrances of *T. darioi* and *T. magnum* in urbanised sites around Montpellier, southern France, over almost 1 year.
3. We did not detect differences in activity between the two species according to temperature, but *T. magnum* was more active than *T. darioi* in winter. Compared to the co-occurring native species, the two *Tapinoma* species were more active at low temperatures and earlier in the year.
4. These results suggest that the difference in invasion success between *T. magnum* and *T. darioi* may not be explained by temperature preference. The difference in activity between native Mediterranean species and invasive *Tapinoma* suggests a coexistence through niche partitioning. In addition, our results suggest that control measures against invasive *Tapinoma* species would be more effective if applied at the end of winter.

KEYWORDS

ants, biological invasions, coexistence, establishment, exploitation competition, foraging

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INTRODUCTION

Invasive species, capable of proliferating rapidly and colonising new environments outside of their native range, are a threat to biodiversity, economy and health worldwide (Diagne et al., 2021; McGeoch et al., 2010; Simberloff et al., 2013). The spread of these species is mainly favoured by global change and the increase in trade and there is no sign that this trend is slowing down on a global scale, particularly in the case of insects (Seebens et al., 2017). However, not all transported species necessarily become invasive, and their invasion success can be compromised at different stages of the process (Williamson & Fitter, 1996). The success of the invasion depends on intrinsic factors (e.g., propagule pressure, or life history traits of the introduced species), as well as the biotic and abiotic conditions of their new environment (Young et al., 2017). The climatic parameters of the invaded area are among the most important abiotic determinants of the establishment of invasive species (Pyšek et al., 2020) and may or may not allow the invasion to succeed by affecting the survival, growth or reproduction of these species (Dijkstra et al., 2017; Lord, 2017; Shi et al., 2010). Sometimes, the introduced invasive species will also be able to establish in the new environment by shifting its ecological niche because of divergent environmental conditions (Bates & Bertelsmeier, 2021; Broennimann et al., 2007; Tang et al., 2021). This phenomenon involves shifts of the introduced species biology (e.g., modification of phenotypic traits, accelerated or delayed phenology, changes in tolerance to environmental parameters).

Once established, these species can modify interspecific interactions by outcompeting native species and disrupting the invaded ecosystem (Didham et al., 2005). However, native species can persist in the invaded area if biological modifications result in minimising the impact of the invasive species on their fitness (Berthon, 2015). To avoid or reduce competition with the invasive species, for example, native species can change their behaviour (Ruland & Jeschke, 2020). Microclimatic and temporal heterogeneity play a role in interspecific interactions between native and invasive species. Depending on environmental or seasonal factors, native species can adjust activity patterns or habitat selection to avoid competition or outcompete invasive species (Gippet et al., 2022; Melbourne et al., 2007; Perales et al., 2021; Valladares et al., 2015). Environmental factors, such as temperature and seasonality, influence foraging and can also allow the coexistence of competing native and invasive species if the preferences of each are different (Albrecht & Gotelli, 2001; Roeder et al., 2018).

To date, over 200 species of ants (out of circa 14,000 described species) are considered as invasive, including 5 species belonging to the top 100 most invasive species worldwide (Bertelsmeier et al., 2018; Lowe et al., 2000). Invasive ants generally share some behavioural characteristics such as the capacity to form supercolonies, which consists of an interconnection of numerous nests (polydomy) housing large numbers of queens (polygyny) and workers (Helanterä, 2022; Moffett, 2012). Some of them are considered as tramp species because they are accidentally introduced by human activities and are harmful to ecosystems (Passera, 1994). Areas

invaded by invasive ant species are therefore often overpopulated by these species to the detriment of other organisms (Gan et al., 2022; Mikissa et al., 2013; Wetterer & Moore, 2005). Invasive ant species are particularly good at locating and exploiting resources, and when foraging they tend to monopolise food sources (Davidson, 1998). These species are often highly competitive and exclude local species through direct aggression or more efficient foraging (Holway et al., 2002).

The *Tapinoma nigerrimum* complex comprises four ant species, *T. darioi*, *T. ibericum*, *T. magnum* and *T. nigerrimum*, all of which originate from the Mediterranean basin. These species are very similar morphologically and were considered as a single species until recently (Seifert et al., 2017). This complex includes three polydomous species (*T. magnum*, *T. darioi* and *T. ibericum*) which can form supercolonies (Seifert et al., 2017). Among the few studies carried out on the ants of this complex, some show the strong competitiveness of *T. magnum* and its negative impact on native ants (Blight et al., 2010; Gippet et al., 2022).

In this study, we focus on *T. magnum* and *T. darioi*, two potential tramp species prevalent in anthropised environments, which appear to be spreading through human activities (Centanni et al., 2022; Lenoir et al., 2023; Seifert et al., 2017). Although they appear very similar morphologically and behaviourally, they differ in their supposed native range and invasion pattern. The supposed native range of *T. magnum* covers North Africa, Italy and the Mediterranean coast of southeastern France. *Tapinoma darioi* has a supposed native range extending from the Mediterranean coast of southwestern France to the northeast of Spain (Centanni et al., 2022; Gouraud & Kaufmann, 2022; Seifert et al., 2017). The two species have been introduced in regions north of the Mediterranean, *T. magnum* having been detected in Belgium, Germany, Switzerland and the Netherlands, *T. darioi* in Switzerland (Dekoninck et al., 2015; Lenoir et al., 2023; Seifert et al., 2017). These species are also invasive in several French localities, even in Mediterranean areas and are in constant expansion (Centanni et al., 2022; Gouraud & Kaufmann, 2022; Lenoir et al., 2023). To date, reports of introductions of these species appear to be limited to urban areas. In addition, Centanni et al. (2022) showed that, in the region of Montpellier, southern France, *T. darioi* occurred more frequently in environments with an intermediate level of urbanisation. Thus, there may be few conservation issues related to the introduction of these species. Nevertheless, it does represent a threat to human activities (e.g., harvest loss in market gardening, disruption of the use of green spaces in cities), as evidenced by the growing number of articles in the local press in mainland France and Corsica. In addition, although *T. darioi* is probably native to the dune environment along the Mediterranean French coast, it thrives in this fragile ecosystem (Centanni et al., 2022), and neither the effect of the introduction of new genetic groups on the dynamics of the species nor the potential consequences on local species in their native range are known yet. In this context, understanding the factors underlying the expansion of *T. darioi* and *T. magnum* would be useful for management strategies.

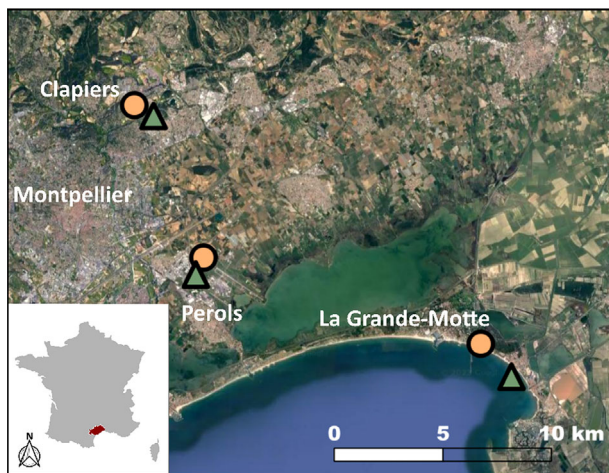


FIGURE 1 Locations of sampling sites in the department of Hérault are marked in red. The green triangles represent *Tapinoma magnum* colonies and the orange discs *Tapinoma darioi* colonies monitored in this study. The map was generated using QGIS 3.28.3.

The two invasive species are present in different proportions in the various areas invaded. For example, Centanni et al. (2022) showed a higher occurrence of *T. darioi* compared with *T. magnum* in southern France. In contrast, *T. magnum* is more common in the northern and colder regions of Europe (Lenoir et al., 2023; Seifert et al., 2017). As ants are ectothermic organisms (Angilletta, 2009; Ruano et al., 2000), temperature is one of the main determinants of their activity, including foraging (Pol & de Casenave, 2004). Given the predominance of *T. magnum* compared to *T. darioi* in the northern regions of Europe and the high acclimatisation capacity of *T. magnum* (Bujan et al., 2021), we hypothesise a difference in thermal preference between the two species. Specifically, we postulate that *T. magnum* is active at lower temperatures than *T. darioi*. If so, this could explain the higher proportion of *T. magnum* in northern localities of Western Europe. Moreover, these invasive species could have an impact on the native ants, and we sought to take a step forward in understanding the interactions of these species with the native species present. Therefore, we aimed to determine whether there was any difference in activity pattern between the two invasive *Tapinoma* species and co-occurring native Mediterranean ants, which could allow the native species to persist in the invaded areas. To answer these questions, we compared foraging activity between invasive *Tapinoma* species at the nest entrance during regular monitoring over almost a year, covering a wide range of temperatures. We also compared the foraging activity of the two invasive *Tapinoma* with that of the other ants present around the *Tapinoma* nest entrances.

MATERIALS AND METHODS

Study area and experimental design

Our study is located in Southern France, in the Hérault department, around the city of Montpellier. The climate is semi-arid Mediterranean. The area in and around the city of Montpellier is highly

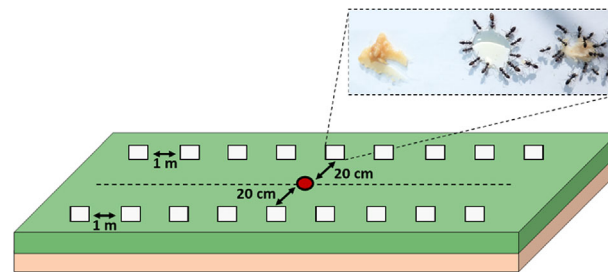


FIGURE 2 Experimental design of the activity measurement protocol. The baits are represented by white squares placed around the central point of activity of the *Tapinoma* colony represented by a red disc.

urbanised and densely populated, with more than 5000 inhabitants per km² (INSEE, 2022).

For activity measurements, three colonies of each species were selected around the city of Montpellier, based on Centanni et al. (2022), who identified colonies at the species level using microsatellite data. *Tapinoma magnum* colonies being rarer around Montpellier (Centanni et al., 2022), three colonies of this species were first selected (*T. magnum* colonies: 43°39'13.9" N 3°55'11.5" E, 43°35'17.8" N 3°56'38.7" E, 43°32'46.0" N 4°07'27.5" E) (Figure 1). Then, to use *T. darioi* colonies exposed to a range of climatic conditions comparable to that of the *T. magnum* colonies, we selected one colony of *T. darioi* close (400–2000 m) to each *T. magnum* colony (*T. darioi* colonies: 43°39'11.6" N 3°54'31.6" E, 43°35'25.2" N 3°56'53.3" E, 43°33'14.3" N 4°06'31.0" E) (Figure 1). The nests were located in green spaces in an urbanised environment: flowerbeds, wasteland and beachside (Table S1).

For each activity measurement, 18 baits were laid out in two parallel lines of 9 baits spaced 1 metre apart, each line being centred on a central point (main entrance of the *Tapinoma* nest), and separated by a distance of 40 cm (Figure 2). Each bait consisted of a strip of paper (11 × 4 cm), on which a drop of honey, tuna rillettes and peanut butter were placed, which are baits commonly used to attract ants (Brinkman et al., 2001; Rahardjo et al., 2023; Wyatt, 2004). After 30 min, the baits with ants were photographed in order to count and identify the ants present (species of the *Tapinoma* colonies were identified in a previous study, see above, and native species were identified on photos). Between 22 and 30 measurement sessions were carried out depending on the colony (147 field sessions in total). The measurement sessions were carried out between autumn 2021 and summer 2022, mostly between January and April (see Figure 3b for the temporal distribution of the sampling).

Soil temperature was measured at the beginning of each foraging activity measurement session at the central point and 50 cm on both sides of this point using a probe thermometer (CookConcept, ±0.5°C) inserted in the ground at a depth of 10 cm, and averaged over the three measurements for each session (Table S2).

Statistical analysis

To test foraging activity of ants throughout the year, activity measurements were processed using generalised additive mixed models

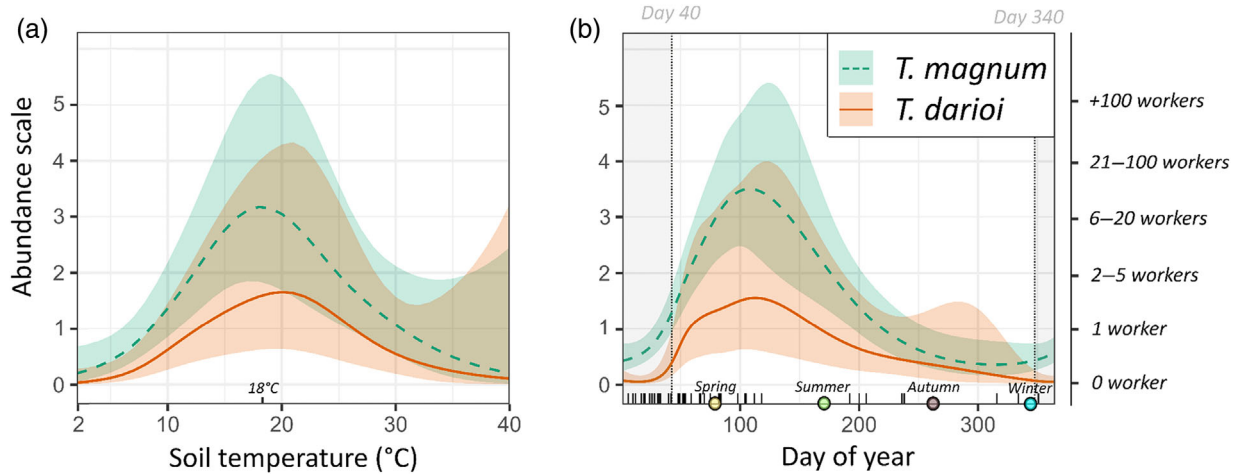


FIGURE 3 Generalised additive mixed model predictions of *Tapinoma magnum* workers (green dotted line, $n = 76$ measurement sessions) and *Tapinoma darioi* workers (orange solid line, $n = 71$ measurement sessions) average abundance scores, with 95% confidence intervals, according to (a) temperature and (b) day of the year (black vertical bars above the x-axis represent sampling days and coloured disk the start of a season). The abundance score of ants is classified into five categories corresponding to the average number of individuals on the 18 baits (0 = 0 worker; 1 = 1 worker; 2 = 2–5 workers; 3 = 6–20 workers; 4 = 21–100 workers; 5 = more than 100 workers). The grey area represents the time period when the activities of *T. magnum* and *T. darioi* differed significantly.

(GAMMs) (Wood, 2006). This semi-parametric model is a flexible regression method for estimating linear and non-linear trends. GAMMs are often used to predict smooth functional relationships between the response variable and the explanatory variables, with the advantage that there are no predefined shape for describing functional relationships (Pedersen et al., 2019; Wood, 2017). Additionally, the foraging activity measurements followed an unevenly spaced time series because the measurement sessions were irregularly spaced in time, which made it difficult to apply conventional time series methods (Simpson, 2018). According to the methods of Andersen (1992), an abundance score (0 = 0 worker; 1 = 1 worker; 2 = 2–5 workers; 3 = 6–20 workers; 4 = 21–100 workers; 5 = more than 100 workers) was calculated for each bait occupied by the ant species considered. Then the average abundance score on the 18 baits was calculated and used as the foraging activity measurement because using the number of individuals recorded yielded overdispersed residuals in the models.

First, independent GAMMs were parameterised for *T. magnum* and for *T. darioi*, respectively, including as response variable the average abundance score and as explanatory variable the mean temperature with the smooth thin plate regression splines term and the site as random effect. Thin plate regression splines can be used to model complex non-linear relationships between variables, smoothing the data efficiently and flexibly without having to specify the location of the nodes (Wood, 2003). Two new GAMMs (one for each species) were parameterised with the same variables, but replacing the mean temperature by the day of the year as explanatory variable with the smooth cyclic cubic spline term. This smoothing term forces the ends of the spline to be equal to each other, allowing continuity between the first and last day of the year (Wood, 2017). In a second phase, the same GAMMs were carried out, considering the activities of both

invasive *Tapinoma* species together to infer their general activity pattern and compare it with that of native species.

This approach provides a reliable estimate by using 95% confidence limits around the modelled responses which we used to determine the differences in activity between ants in different categories (i.e., *T. magnum* vs. *T. darioi* and *Tapinoma* vs. native ants). For all the models, the distribution of the specified errors was quasi-Poisson. Model parameters were chosen by restricted maximum likelihood (REML) selection. All the GAMMs were produced using the ‘gam’ function in the ‘mgcv’ package (Wood, 2011) using R 4.2.1 software (R Core Team, 2022) and R studio (RStudio Core Team, 2020).

RESULTS

Species detected on baits

Overall, nine genera other than *Tapinoma* were recorded on the baits: *Camponotus*, *Crematogaster*, *Lasius*, *Messor*, *Monomorium*, *Pheidole*, *Plagiolepis*, *Temnothorax* and *Tetramorium*. The number of genera per site varied between 3 and 7 including *Tapinoma* (mean = 4.2).

Differences in activity between *T. magnum* and *T. darioi*

The GAMMs of *T. magnum* and *T. darioi* representing the average abundance score as a function of temperature explain 46.4% and 48.3% of the deviance respectively (Figure S1). For *T. magnum*, temperature and site had a significant effect on the average abundance score ($p < 0.001$ and $p = 0.01$). For *T. darioi*, temperature and site had

a significant effect on the average abundance score ($p < 0.001$ and $p = 0.02$). Along the observed temperature gradient, the average abundance score did not differ significantly between *T. magnum* and *T. darioi*. The maximum levels of activity for *T. magnum* and *T. darioi* were 3.2 and 1.7 of average abundance score, respectively, although these maximum levels of activity were not significantly different (Figure 3a). The activity of both species was highest between 18 and 20°C.

The GAMMs of *T. magnum* and *T. darioi* representing the average abundance score according to the day of the year explain 55.5% and 74.4% of the deviance respectively. For *T. magnum*, the day of the year had a significant effect on the average abundance score ($p < 0.001$), but the site did not ($p = 0.07$). For *T. darioi*, the day of year and site both had a significant effect on the average abundance score ($p < 0.001$ and $p = 0.001$, respectively). The average abundance score differed significantly between *T. magnum* and *T. darioi* over the period from day 340 to day 365 and from day 1 to day 40 of the year (early December to mid-February, i.e., autumn–winter). Over this period, *T. darioi* had an average abundance score close to 0. In contrast, *T. magnum* was active throughout the year with a minimum average abundance score at 0.5. The average abundance score of *T. magnum* and *T. darioi* began to increase from day 340 (early December, i.e., autumn) and day 30 (early February, i.e., winter) of the year, respectively. Both species reached their peak activity on day 100 (mid-April, i.e., spring), and then the average abundance score decreased throughout the year, however, the peak activity of *T. magnum* (3.6) was not significantly higher than that of *T. darioi* (1.6) (Figure 3b).

Differences in activity between *Tapinoma* and the native ant species

The GAMMs for *Tapinoma* and native species, representing the average abundance score as a function of temperature, explain 52.3% and 90.2% of the deviance, respectively (Figure S1). For *Tapinoma* and native species, temperature and site had a significant effect on the average abundance score ($p < 0.001$ in both cases). Along the temperature gradient observed, the average abundance score by *Tapinoma* was significantly higher than that of native species for the range of lowest temperatures (6–19°C). *Tapinoma* activity increased strongly from 3 to 20°C where it reached a maximum (2.3 of average abundance score) and then decreased, while native species activity increased slowly from 7 to 27°C where it reached a maximum (1 of average abundance score) and then decreased. The two peaks of activity are significantly different (Figure 4a).

The GAMMs for *Tapinoma* and native species representing the average abundance score according to the day of the year explain 66.9% and 88.8% of the deviance respectively. For *Tapinoma* and native species, day of year and site had a significant effect on the average abundance score ($p < 0.001$ in both cases). The average abundance score by *Tapinoma* was significantly higher than that of native species over the period from day 30 to day 120 of the year

(early February to end April, i.e., winter–spring). The average abundance score by *Tapinoma* increased from day 10 to day 100 (mid-January to mid-April, i.e., winter–spring), when it peaked (2.3 of average abundance score), and then decreased. The average abundance score by native ants increased from day 70 to day 250 (mid-March to early September, i.e., spring–summer), when it reached a maximum (1.1), and then decreased. The two activity peaks are significantly different (Figure 4b).

DISCUSSION

In this study, we show how temperature and season regulate the activities of *T. darioi* and *T. magnum*, as well as native species in an invaded Mediterranean environment. We observed a similar range of temperature of activity between *T. darioi* and *T. magnum*. However, *T. magnum* was more active than *T. darioi* in winter, which may indicate the influence of seasonal factors other than temperature. We were able to identify differences in activity between *Tapinoma* and native species depending on the temperature or the season following in situ activity measurements throughout the year.

Establishment success of *T. magnum* and *T. darioi*

Temperature is a major determinant of the distribution and ability of ants to establish new populations throughout the world (Jung et al., 2021; Roeder et al., 2018; Warren II & Chick, 2013). It has also been established that the temperature-dependent activity niche plays a crucial role in ant distribution, even superseding the importance of critical thermal limits in some cases (Guo et al., 2020). Our results highlighted *Tapinoma* activity under a wide range of temperatures, including relatively cold temperatures, potentially explaining the establishment of these species in regions that are colder than their native range (Dekoninck et al., 2015; Noordijk, 2016; Seifert et al., 2017). Furthermore, Noordijk (2016) also observed sunbathing activity of these *Tapinoma* in winter in the Netherlands, which confirm that these ants are active at cold temperatures even in invaded northern European locations. With ongoing climate change and its positive impact on the spread of invasive ants (Bertelsmeier et al., 2015, 2016), these two species represent a major threat on a very large scale.

In this study, we did not detect any difference in activity between the two species according to temperature. According to our results, the differences in distribution between the two species in Western Europe (Gouraud & Kaufmann, 2022; Lenoir et al., 2023; Seifert et al., 2017) may therefore not be explained by foraging temperature preferences. Nevertheless, we observed differences in activity between the two species in winter that were not explained by temperature. Other climatic parameters involved in seasonality, such as humidity or photoperiod, are known to influence ant activity (KimFung & ChowYang, 2009; Lei et al., 2019) and may play a role in the establishment of these species. However, due to the limited

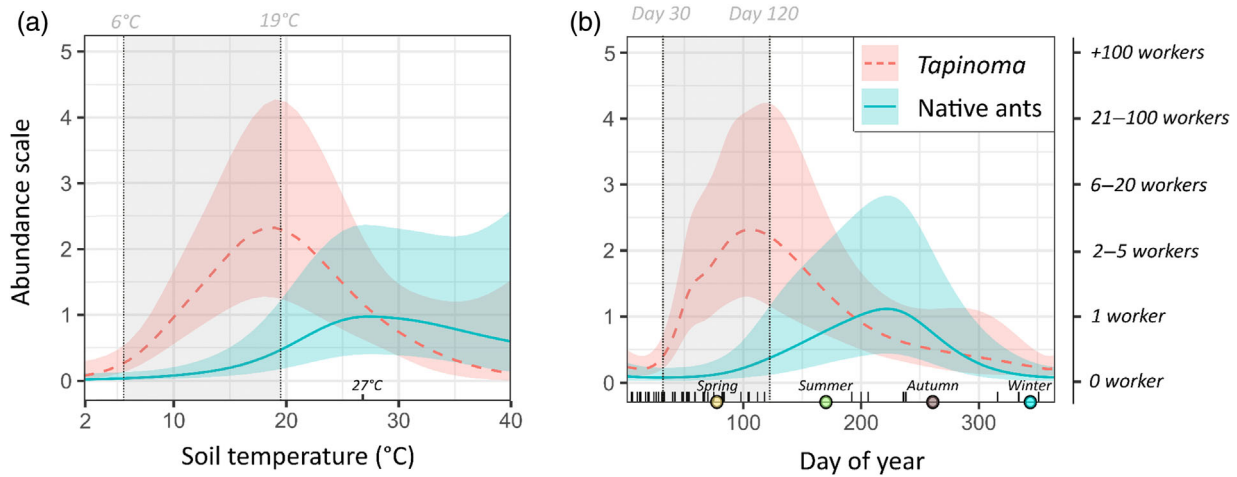


FIGURE 4 Generalised additive mixed model predictions of *Tapinoma* workers (red dotted line) and native ant workers (blue solid line) ($n = 147$ measurement sessions) average abundance scores, with 95% confidence intervals, according to (a) temperature and (b) day of the year (black vertical bars above the x-axis represent sampling days and coloured disk the start of a season). The abundance score of ants is classified into five categories corresponding to the average number of individuals on the 18 baits (0 = 0 worker; 1 = 1 worker; 2 = 2–5 workers; 3 = 6–20 workers; 4 = 21–100 workers; 5 = more than 100 workers). The grey area represents the temperature range and the time period when the activities of *Tapinoma* and native species differed significantly.

number of colonies of each *Tapinoma* species observed, we must remain cautious about these results.

Our results support the hypothesis that climatic parameters such as temperature have little influence on the difference in establishment between these species in continental Europe. Biotic factors, such as competition, could better explain the difference in establishment between *T. magnum* and *T. darioi* depending on locality (de Soares, 2013; Ribas & Schoereder, 2002). These two species seem to share similar temperature niches and type of environment (anthropised environment) (Centanni et al., 2022; Gouraud & Kaufmann, 2022), so they may be strong competitors. Thus, the difference in establishment between the two invasive *Tapinoma* species in non-native areas could have more to do with differential introduction patterns (Destour et al., in prep). One hypothesis would be that the species that is established into a given environment would be the species that has been introduced first, as it would have no competitors in the invaded environment and would then exclude the other by competitive exclusion (priority effect) (Cleland et al., 2015; Fukami, 2015; Weidlich et al., 2021). In addition, Palmer et al. (2002, 2003) demonstrated that in ants, priority effect can allow an ant species to avoid the exclusion by another ant species whatever the competitive hierarchy between them. On the other hand, *T. magnum* is more active in winter than *T. darioi*. This species therefore appears to be better able to compete with non-Mediterranean species than *T. darioi*, which could facilitate its establishment in northern Europe.

Niche partitioning between *Tapinoma* and native ants

We observed that the peak activity of *Tapinoma* occurred at a lower temperature and earlier in the season from that of native species.

This difference, which allows different activity niches to be occupied, may explain the coexistence of *Tapinoma* and native species (Gippet et al., 2022). For the origin of this difference in activity periods, we know that workers of the *T. nigerrimum* complex are generally active relatively early in the year compared with other Mediterranean species (Carpintero et al., 2007; Cros et al., 1997). The swarming period of these *Tapinoma* species starts at the end of spring, so their colonies probably need more resources just before this period than species with a later swarming period. The other Mediterranean species observed in this study have a swarming period between late spring and early autumn (Blatrix et al., 2013). The period of peak activity of *Tapinoma* species, which is initially out of sync with other species, may be a factor that facilitates their establishment in invaded areas. In fact, such a phenology could enable them to avoid competition with dominant native species able to limit the establishment of invasive species (Cordonnier et al., 2020; Krushelnicky & Gillespie, 2010; Wetterer et al., 2006). *Tapinoma magnum* has the ability to shift its thermal niche (Bujan et al., 2021), potentially accentuating this difference in activity periods (Broennimann et al., 2007). We cannot tell from our results whether the timing of the peak activity we observed for *T. magnum* was intrinsic to the species, or induced or accentuated by a niche shift following its introduction. The difference in activity observed between *Tapinoma* and native ants may also be due to a shift in the activity period of native species caused by the presence of *Tapinoma*. Furthermore, the difference in activity periods, due to temporal heterogeneity, may not be the only difference that allows coexistence of native ants and *Tapinoma* species. Gippet et al. (2022) showed that heterogeneity in microclimatic conditions could also play an important role in coexistence in areas invaded by *T. magnum*.

Management implications

Tapinoma is spreading rapidly, particularly through the transport of ornamental plants, and more and more populations are being established in Europe (Gouraud & Kaufmann, 2022; Lenoir et al., 2023; Seifert et al., 2017). Given its negative impact on local ants and the potential damage caused by the formation of supercolonies (Gippet et al., 2022; Helanterä, 2022), it is becoming essential to eradicate or at least control populations established in non-native areas. However, the eradication of invasive ants often requires the use of toxic baits, representing a danger for the native fauna of the invaded locality (Hoffmann et al., 2016). To minimise the impact of these toxic baits, we should consider applying them during periods when native ants are less active, or even inactive (Hoffmann et al., 2011). Planning an eradication for late winter could be beneficial for the effective elimination of *Tapinoma*, as their activity peaks at this time, sparing other native ants that are less active during this period in Mediterranean areas.

However, we should be aware that the eradication success rate for ants is relatively low (66%), that is 20% lower than for invasive mammals on islands (Hoffmann et al., 2016). Therefore, it is advisable to focus on managing invasion routes rather than investing in eradication attempts (Hulme, 2009; Pergl et al., 2017).

AUTHOR CONTRIBUTIONS

Giovanny Destour: Data curation; formal analysis; writing – original draft; writing – review and editing. **Rumsais Blatrix:** Supervision; conceptualization; methodology; writing – review and editing; funding acquisition; formal analysis; data curation. **Aurélien Caries:** Writing – review and editing; investigation. **Juliette Genevet:** Investigation; writing – review and editing. **Bernard Kaufmann:** Conceptualization; writing – review and editing; data curation; methodology. **Baptiste Lecoq:** Investigation; writing – review and editing. **Annick Lucas:** Investigation; writing – review and editing. **Killian Verlingue:** Investigation; writing – review and editing. **Alan Vergnes:** Conceptualization; writing – review and editing; formal analysis; data curation; supervision; funding acquisition; methodology. **Marion Javal:** Conceptualization; methodology; funding acquisition; writing – review and editing; formal analysis; supervision; project administration.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.


DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supplementary material of this article.

ETHICS STATEMENT

The authors have respected ethical standards in the preparation of this article.

ORCID

Giovanny Destour  <https://orcid.org/0009-0002-5725-5816>
 Rumsais Blatrix  <https://orcid.org/0000-0003-1662-7791>
 Aurélien Caries  <https://orcid.org/0009-0002-9507-7475>
 Bernard Kaufmann  <https://orcid.org/0000-0001-9097-3452>
 Baptiste Lecoq  <https://orcid.org/0009-0005-2834-9436>
 Alan Vergnes  <https://orcid.org/0000-0002-6128-0793>
 Marion Javal  <https://orcid.org/0000-0001-7878-2936>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Mean worker abundance (\pm SE) depending on temperature categories for (A) *T. darioi* (orange) and *T. magnum* (green) (B) *Tapinoma* (red) species and native species (blue).

Table S1. Characteristics of sampled sites.

Table S2. Raw data related to activity measurements. «temp air beginning» and «temp air end» indicate the air temperature at the beginning and the end of each measurements; «temp ground middle», «temp ground right» and «temp ground left» represent the temperature measured 10 cm below the ground at the central point and on the two sides respectively; «type of bait» can either be honey (H), peanut butter (P) or tuna rillettes (T).

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