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Genetic tracing reveals the role of ornamental plant trade in the simultaneous spread of three invasive ant species in Western Europe

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ABSTRACT

Understanding how human activities trigger biological invasions is crucial to prevent the environmental and socioeconomic costs of invasive species. The *Tapinoma nigerrimum* complex comprise four species of ants, three of which (*T. darioi*, *T. ibericum*, *T. magnum*) exhibit biological and ecological characteristics of invasive ant species. These three species are native to Western Mediterranean Europe and North Africa, but have been reported as invasive in northern Europe and in the French Mediterranean region. The trade in ornamental plants is a common invasion pathway for many taxa, but its role in the continental spread of invasive *Tapinoma* species remains unknown. This study aims to identify the role of Ornamental Plant Sales Outlets (OPSOs) in the introduction of these three species and to determine the geographical origin of populations present in French OPSOs. *Tapinoma* colonies were sampled in 103 OPSOs across five French urban areas, with a specific focus on the Mediterranean region. Collected ant workers were identified to the species level using 15 microsatellite markers. Genotypes were compared to genetic profiles of European and North African populations to trace the geographical origin of introduced populations. We found a high prevalence of invasive species in OPSOs, with 66% (16/24) of invaded OPSOs in the urban area of Montpellier and 31% (19/61) in the urban area of Lyon, suggesting an important role of OPSOs in the introduction of the three species. Multiple introductions were detected in Montpellier OPSOs, at species level (seven OPSOs with two or three invasive species) and between genetic clusters within species (five OPSOs with more than one genetic cluster for *T. magnum*). Based on genetic clustering, populations with probable origins in Spain or Italy were detected in the French OPSOs. These results are particularly worrying as multiple simultaneous introductions might promote a rapid genetic recovery from founder effects for one species or result in hybridization between species. Overall, our findings highlight the importance of the trade in ornamental plants in shaping insect invasions and increasing the risk of genetic mixing with unforeseeable consequences on species invasiveness.

Keywords: Biological invasion ; Garden centres ; Microsatellites ; Plant nurseries ; *Tapinoma darioi* ; *Tapinoma ibericum* ; *Tapinoma magnum*

1. Introduction

85 Understanding and preventing biological invasions is crucial because
86 they are among the leading causes of the ongoing biodiversity crisis, and
87 threaten human health and societies (McGeoch et al., 2010; Pyšek &
88 Richardson, 2010; Diagne et al., 2021). Human activities, by introducing
89 species into new habitats, are the main cause of biological invasions globally
90 (van Kleunen et al., 2015; Bonnamour et al., 2021). Among the many species
91 transported by humans at global scale, some are able to establish and thrive
92 in novel environments, potentially spreading beyond their initial introduction
93 point and causing damages (Broennimann et al., 2007; Young et al., 2017;
94 Pyšek et al., 2020; Fenn-Moltu et al., 2023). Insects, because of their small size,
95 are easily unintentionally transported by human activities through the
96 contamination of traded materials or by hitchhiking on vehicles (Meurisse et
97 al., 2019; Gippet et al., 2019).

98 Ants are among the most destructive invasive animal species, causing
99 harm not only to biodiversity but also generating important socio-economic
100 impacts (e.g. health issues, agricultural losses, costs of control and
101 eradication) (Lach & Thomas, 2008; Silverman & Brightwell, 2008). For
102 example, the fire ant *Solenopsis invicta* and the little fire ant *Wasmannia*
103 *auropunctata* have cost billions of USD in damages and control efforts in the
104 last decades (Angulo et al., 2022). Most invasive ant species can occupy
105 various environments and exploit a large quantity and diversity of resources
106 within their new environments (Crowder & Snyder, 2010; Felden et al., 2018;
107 Balzani et al., 2021). Furthermore, these species often form polygynous and
108 polydomous (i.e. multiple-queen, multiple-nest) colonies, conducive to the
109 formation of supercolonies (Bertelsmeier et al., 2015; Helanterä, 2022). These
110 supercolonies expand through budding, a process by which queens (and some
111 workers) establish new nests close to the main colony while maintaining their
112 connection to other nests (by exchanging workers) and thus preserving social
113 recognition within the entire supercolony (Torres et al., 2007; Moffett, 2012;
114 Helanterä, 2022). Supercolonies can cover large areas, with a high density of
115 workers exploiting available resources (Gippet et al., 2018). For example, some
116 supercolonies of *Lasius neglectus* can reach >20ha (Ugelvig et al., 2008;
117 Gippet et al., 2022).

118 The *Tapinoma nigerrimum* complex comprises four ant species, *T. darioi*,
119 *T. ibericum*, *T. magnum* and *T. nigerrimum*, all of which originate from the
120 Western Mediterranean area (i.e. from Spain to Italy and Morocco to Tunisia).
121 These species are very similar morphologically and were considered to be a
122 single species until the recent re-evaluation of this complex and its subsequent
123 revision (Seifert et al., 2017, 2024). This complex comprises three polydomous
124 species, which are capable of forming supercolonies (*T. darioi*, *T. ibericum*, *T.*
125 *magnum*), and two monodomous species (*T. nigerrimum* and *T. hispanicum*)
126 (Seifert et al., 2017, 2024). The three polydomous species have a great
127 invasive potential as they can be common in anthropised environments and
128 appear to be spreading through human activities (Seifert et al., 2017; Centanni
129 et al., 2022; Lenoir et al., 2023). They also pose a threat to human activities
130 and to native ants (Mansour et al., 2012; Gippet, George, et al., 2022; Gouraud
131 & Kaufmann, 2022; Lenoir et al., 2023). *Tapinoma nigerrimum* and *T.*
132 *hispanicum* which feature no traits associated with invasiveness, can
133 respectively be found in southern France/northern Spain and southern/western
134 Spain (Seifert et al., 2017, 2024). The probable native range of *T. magnum*

135 encompasses eastern and southern Italy and North Africa (Seifert et al., 2017;
136 Gouraud & Kaufmann, 2022). The situation in northern Italy and the
137 Mediterranean coast of France is unclear, but may be due to an earlier range
138 expansion of *T. magnum* (Seifert et al., 2024). *Tapinoma darioi* has a probable
139 native distribution in North-East Spain and the French Mediterranean coast.
140 *Tapinoma ibericum* is found in the southern and western Iberian peninsula
141 including Spain and Portugal (Seifert et al., 2017; Gouraud & Kaufmann, 2022).
142 In addition, these three species have been introduced into northern Europe.
143 The first proven record for *T. magnum* out of its native range was in Edesheim,
144 Germany in 2009 (Seifert et al. 2017) and the species is now present in Austria,
145 Belgium, England, Germany, Switzerland and the Netherlands. *Tapinoma darioi*
146 was detected in the Netherlands and *T. ibericum* in England, Germany and the
147 Netherlands (Dekoninck et al., 2015; Seifert et al., 2017, 2024; Lenoir et al.,
148 2023). These species are also invasive in several Mediterranean and northern
149 French localities, where they exhibit invasive behaviour (Blight et al., 2010;
150 Centanni et al., 2022; Gouraud & Kaufmann, 2022; Lenoir et al., 2023). The
151 three invasive species are present in different proportions in the invaded areas,
152 suggesting different patterns of introduction. In the urban area of Montpellier
153 (Mediterranean France), for example, Centanni et al., (2022) show a strong
154 abundance of *T. darioi* compared with the other two invasive species. On the
155 other hand, in the northern parts of France and Europe, *T. magnum* is the most
156 common species (Seifert et al., 2017; Lenoir et al., 2023).

157 The European spread of invasive *Tapinoma* species is suspected to occur
158 mostly through the trade in ornamental plants (Seifert et al. 2024, Gouraud &
159 Kaufmann, 2022). For example, *Tapinoma* ants have been detected in pots of
160 olive trees in Pays de la Loire (north-west France) and Gironde (west France)
161 departments (Gouraud & Kaufmann, 2022; Lenoir et al., 2023). Yet, the role of
162 the trade in ornamental plants in shaping ongoing invasions of *Tapinoma*
163 species remains unexplored. More generally, because it is still incipient,
164 studying this invasion could provide invaluable insights into one of the most
165 common pathways for insect invasions.

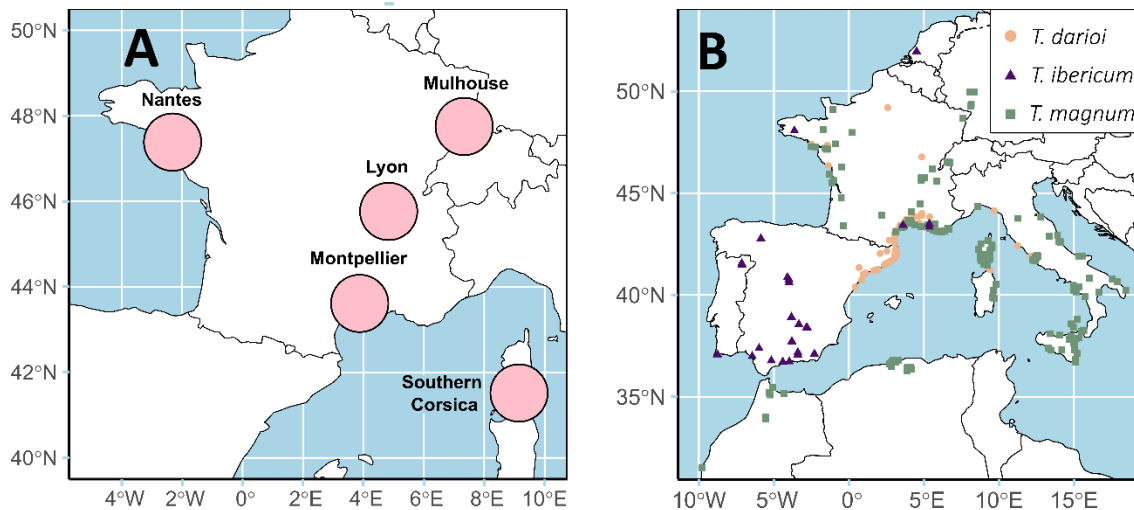
166 In this study, we focused on the ongoing invasion of *T. darioi*, *T. ibericum*
167 and *T. magnum* in Western Europe. Our objective was to evaluate the role of
168 Ornamental Plant Sales Outlets (OPSOs) as an introduction pathway for ant
169 invasions using genetic tools. We collected and genotyped *Tapinoma* workers
170 from OPSOs in five French urban areas with a specific focus on the Montpellier
171 (Mediterranean coast), and analysed their relationships to workers from a large
172 number of localities of the distribution range of the three species. This allowed
173 us to determine species identity, define genetic groups within species and infer
174 the broad geographical origins of the *Tapinoma* ants found in OPSOs.

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2. Material and methods

177 2.1. Study sites and sampling



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Figure 1 - (A) Location of the French urban areas where OPSOs were sampled. **(B)** Distribution of samples of *T. darioi* (orange dots), *T. ibericum* (purple triangles), *T. magnum* (green squares) collected in different localities of western Europe and North Africa and used in this study.

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Systematic sampling of OPSOs was carried out in three French urban areas (Montpellier, Lyon, Mulhouse). Two opportunistic samples from OSPOs in Nantes urban areas and southern Corsica were added to the dataset (**Fig. 1A**). The OPSOs were selected to sample a broad range of plant sellers (plant nurseries or garden centres). OPSO sampling was carried out by different teams at different times in the five urban zones resulting in different protocols described below.

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In the Montpellier urban area (French Mediterranean bioregion) 24 OPSOs were sampled in March-April 2023. Two sampling perimeters were defined for each OPSO. The indoor perimeter consisted of all areas where the activities of the retailers were concentrated (greenhouses, outdoor pots, storage and composting areas). The outdoor perimeter surrounded the indoor perimeter and extended over 15 metres. Within each of the two sampling perimeters, 20 baits consisting of a strip of paper (11x4cm) on which a drop of honey were randomly distributed (Delabie et al., 2021). After one hour, the workers found on the baits were collected manually or using a mouth aspirator. Baiting was combined with one hour of visual prospection during which all the *Tapinoma* workers detected were collected. Several *Tapinoma* samples were analysed for each OPSO.

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In the Lyon urban area (South of French continental bioregion) 61 OPSOs were sampled in spring 2019 and in the Mulhouse urban area (North of French continental bioregion) 16 OPSOs were sampled in summer 2019. The OPSOs were searched by visual prospection inside and outside, in all areas open to the public including greenhouses and open air plant nurseries. Only one *Tapinoma* sample was collected per OPSO in Lyon, but not in Mulhouse.

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In the Nantes urban area (Oceanic bioregion) and southern Corsica (Mediterranean Island), only 1 sample was collected by visual prospection in 1 OPSO in each urban area (**Fig. 1A**).

In parallel, from 2009 to 2023, *Tapinoma* workers were collected during systematic (e.g. Centanni et al. 2022) and opportunistic sampling at various sites in Europe and North Africa, which we will refer to as “localities” in the remainder of this manuscript (**Fig. 1B**).

215 2.2. DNA extraction and Genotyping

216 DNA was extracted from workers of the *Tapinoma nigerrimum* complex
217 collected from OPSOs (n = 234) and from different localities (n = 486) by
218 grinding each worker in proteinase K (10 µL at 15 mg/ml) and Chelex 7% (150
219 µL). After grinding, samples were incubated at 55°C for 2 hours, followed by a
220 further 15 minutes at 90°C to inactivate the proteinase K.

221 To identify the species of individuals collected and to assign them to genetic
222 groups, 15 microsatellite markers specifically developed for the *Tapinoma*
223 *nigerrimum* complex were selected and pooled into three genotyping
224 multiplexes (Centanni et al., 2022). The three PCR mixes consisted of 6 µl of
225 Master Mix Type-it microsatellite PCR kit (QIAGEN, 206246, Hilden, France), 3.6
226 µl of H₂O, 2 µl of DNA from each sample collected and 0.4 µl of forward primer
227 + reverse primer + tails. Forward primers were end-labelled with universal tails
228 according to Blackett et al., (2012), using fluorescent dyes. PCR of the three
229 genotyping mixes was carried out using the following PCR programme: 5 min
230 denaturation at 95°C, then 32 cycles with denaturation (30 s) at 95°C,
231 annealing (3 min) at 60°C, and extension (30 s) at 72°C, and a final extension
232 of 30 min at 60°C. Finally, a 30-minute migration of the PCR products on an
233 agarose gel (3%) was carried out to check the quality of the amplification. All
234 the PCR products were then analysed in a 3730xl DNA analyser (Applied
235 Biosystems) by a service provider (GENTYANE, Clermont-Ferrand, France).
236 Electropherograms were read and interpreted using Genemarker 1.95 software
237 (Softgenetics, State College, PA, USA).

238 2.3. Species identification and comparison of occurrences

239 Genetic clusters using all individuals were defined using a combination
240 of two analytical methods: simple PCA (Jombart et al., 2010) and Bayesian
241 clustering (STRUCTURE program, Pritchard et al., 2000), using a similar method
242 as Centanni et al. (2022). Species names were assigned to these clusters based
243 on the multilocus microsatellite genotypes of reference individuals identified
244 in Seifert et al. (2017).

245 In the present study, an occurrence was defined as the presence of at
246 least one individual of a species in an OPSO or in one point of the standardised
247 grid in Centanni et al. (2022). We tested whether the proportion of occurrences
248 of species of the *Tapinoma nigerrimum* complex differed between outdoor and
249 indoor perimeter of the OPSOs using a χ^2 compliance test. We also tested if
250 OPSOs samples were similar to samples from Centanni et al. (2022) with an
251 additional χ^2 .

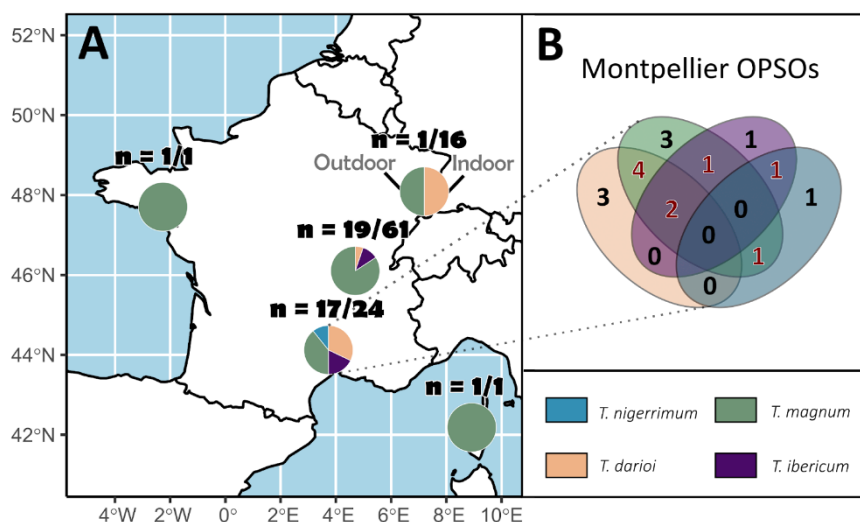
252 2.4. Assessment of OPSOs population structure and identifying source 253 populations of OPSOs

254 The genetic structure of the populations within each species was
255 analysed by Bayesian clustering using STRUCTURE 2.3.4 (Pritchard et al.,
256 2000). Clustering analysis was realised in two steps, consisting in a series of
257 three analyses, one for each *Tapinoma* species (Appendix 1). Firstly, a
258 STRUCTURE analysis was performed using only the OPSOs samples to
259 determine whether there were one or more genetic groups within each OPSO

260 and to know if the outdoor populations were the same as the indoor
 261 populations. Then, a second STRUCTURE analysis was performed in order to
 262 identify the potential source populations of the OPSOs. For this second step,
 263 we used a dataset consisting of samples from various localities in Western
 264 Europe and North Africa. This dataset included either 179 samples of *T. darioi*
 265 species, 234 samples of *T. magnum* species, or 30 samples of *T. ibericum*
 266 species, which served as the reference source populations. We included one
 267 individual (selected randomly) per genetic group and per OPSO, which were
 268 the specimens whose origin was to be determined. Not all specimens from
 269 OPSOs were used to avoid potential bias in Bayesian analysis. For each
 270 STRUCTURE analysis, an admixture model was built using a burn-in period of
 271 250,000 iterations, followed by 250,000 MCMC (Markov Chain Monte Carlo)
 272 iterations. For each potential number of genetic groups, denoted as K (ranging
 273 from 1 to 10) (Pritchard et al., 2000), a total of 15 independent runs were
 274 executed. For each STRUCTURE analyses the K values were selected using
 275 three criteria : high Evanno's ΔK (Earl & vonHoldt, 2012), high mean similarity
 276 between the runs and small number of minor clusters. The admixture models
 277 obtained from these analyses were then compiled using CLUMPAK (Kopelman
 278 et al., 2015) which provides consensus between similar runs generated by
 279 STRUCTURE. The spatial distribution of genotypes for samples from the various
 280 localities was then mapped out using QGIS 3.28.3, using the compilation of the
 281 runs from STRUCTURE built in CLUMPAK during the second analysis.

282 283 284 285 3. Results

286 3.1. Occurrences of *Tapinoma* species in OPSOs



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288 **Figure 2** - (A) Proportion of occurrences of *Tapinoma nigerrimum*
 289 complex species in French OPSOs (*n* = number of OPSOs colonised / total
 290 number of OPSOs visited) (B) Venn diagram showing occurrences (black
 291 numbers) and co-occurrences (red numbers) of *T. magnum*, *T. darioi* and
 292 *T. ibericum* in 17 Montpellier OPSOs (in the other areas only one sample

293 was collected per OPSO, and thus, co-occurrences could not be
294 investigated).

295 An important proportion of OPSOs featured *Tapinoma* species (37.8%).
296 Where systematic sampling was carried out, the presence of *Tapinoma* species
297 in OPSOs varied strongly depending on urban areas: 70.8% in Montpellier;
298 31.1% in Lyon; 6.3% in Mulhouse. Over the 103 sampled OPSOs, *T. magnum*
299 was the most frequently found with 30 occurrences (29.1%), *T. darioi* was
300 found in 11 OPSOs (10.7%), *T. ibericum* in 7 OPSOs (6.8%) and *T. nigerrimum*
301 3 OPSOs (2.9%) (**Fig. 2A**).

302 3.2. Bait occupancy and occurrences of *Tapinoma* species in Montpellier

303 Among the baits of 24 OPSOs in Montpellier, an average of 5.5 baits out
304 of 20 were visited by ants indoors, and 6.5/20 outdoors. Across these baits, 28
305 native species and 2 exotic species (*Plagiolepis schmitzii*, *Lasius neglectus*)
306 were collected, with 26 species indoors and 20 species outdoors (Appendix 2).
307 Native species dominated bait occupancy, accounting for 86.4% of the
308 occupied baits, followed by species from the *Tapinoma nigerrimum* complex
309 (12.7%) and two other exotic species (0.9%). The majority of *Tapinoma*
310 *nigerrimum* complex workers collected for the study were sampled through
311 active prospection (78%).

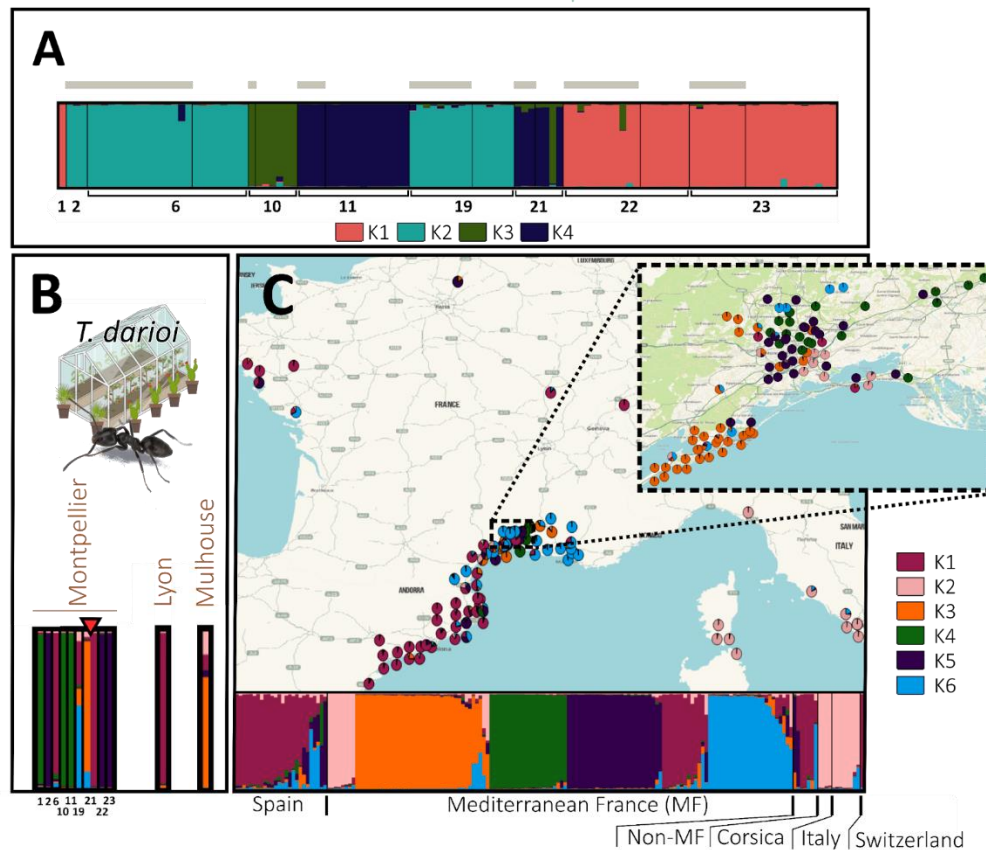
312 Seven OPSOs were colonised simultaneously by more than one invasive
313 *Tapinoma* species: 2 by *T. darioi*, *T. ibericum* and *T. magnum*, 4 by *T. darioi*
314 and *T. magnum* and 1 by *T. ibericum* and *T. magnum*. *Tapinoma nigerrimum*
315 was also found co-occurring, once with *T. ibericum* and once with *T. darioi*.
316 (**Fig. 2B**). The indoor perimeters of 17/24 OPSOs were colonised by at least
317 one species from the *Tapinoma nigerrimum* complex. In the 24 OPSOs, there
318 were 8 occurrences (one occurrence = at least one individual of one species
319 regardless of the sampling method in one OPSO) of *T. darioi* (32%), 5
320 occurrences of *T. ibericum* (20%), 10 occurrences of *T. magnum* (40%), and 2
321 occurrences of *T. nigerrimum* (8%). The outdoor perimeter of 14/24 OPSOs
322 presented at least one *Tapinoma nigerrimum* complex species: 8 occurrences
323 of *T. darioi* (47%), 1 occurrence of *T. ibericum* (5.9%), 6 occurrences of *T.*
324 *magnum* (35.3%), and 2 occurrences of *T. nigerrimum* (11.8%). The relative
325 proportions of the four species discovered in the indoor and outdoor perimeter
326 OPSOs did not differ significantly ($\chi = 0.41$, $P = 0.82$). In the Montpellier OPSOs
327 a total of 211 workers of the *Tapinoma nigerrimum* complex were genotyped,
328 consisting of 111 *T. darioi*, 19 *T. ibericum*, 70 *T. magnum* used for STRUCTURE
329 analysis (1 individual corresponding to 1 bar) and 11 *T. nigerrimum* (Appendix
330 3).

331 In contrast, in the localities of Montpellier (not taking into account OPSOs
332 sampling), for 926 sampling point, occurrences were as follows: 78 *T. darioi*
333 (27.8%), 1 *T. ibericum* (0.3%), 6 *T. magnum* (2.1%) and 197 *T. nigerrimum*
334 (69.8%) (Centanni et al., 2022). The relative proportions of the four species
335 discovered in the indoor and outdoor perimeter OPSOs differed significantly
336 from those sampled in Montpellier localities ($\chi = 20.32$, $P = 0.00004$ for indoors
337 and $\chi = 6.90$, $P = 0.03$ for outdoors). The proportion of *T. magnum*, *T. darioi*
338 and *T. ibericum* is higher than expected, while the number of *T. nigerrimum*
339 est lower than exempted in OPSOs.

340 In the 31.1% OPSOs colonised in Lyon, there were 1 occurrence of *T.*
341 *darioi*, 2 occurrences of *T. ibericum* and 16 occurrences of *T. magnum*. In the

342 localities of Lyon (not taking into account OPSOs sampling), for 1248 sampling
 343 points, occurrences were as follows : 0 *T. darioi*, 0 *T. ibericum*, 2 *T. magnum*
 344 (unpublished data from Gippet et al., 2017).

345 3.3. Structure of *T. darioi* populations and putative source populations of
 346 OPSOs

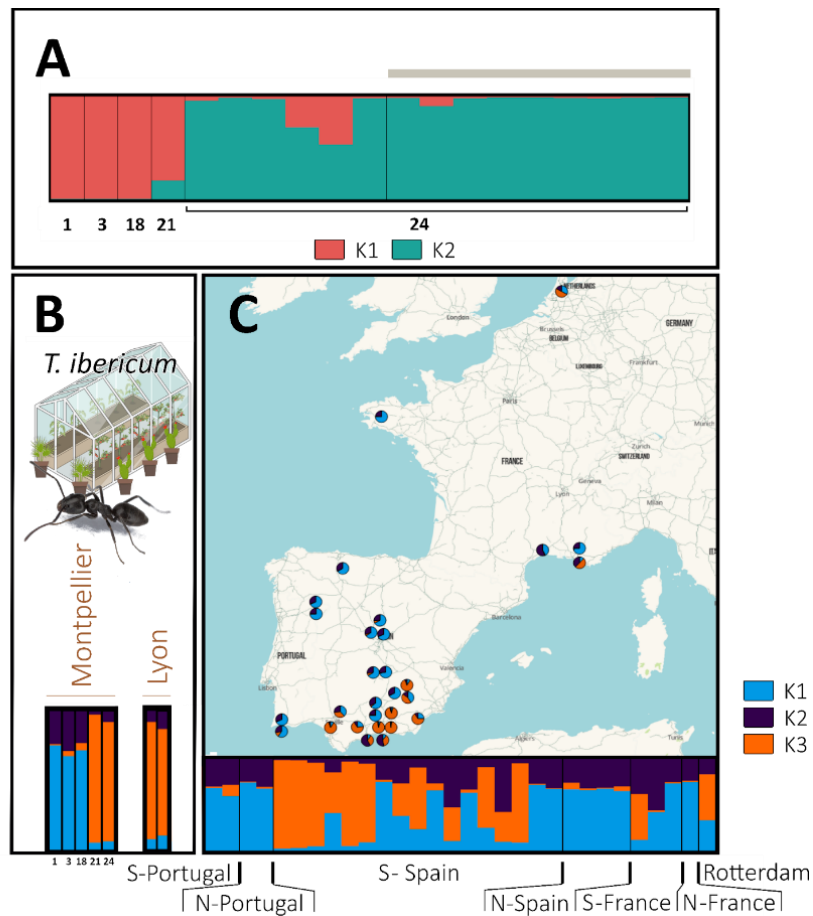


347
 348 **Figure 3** - Population genetic structure of *T. darioi*. In barplots, each individual
 349 is represented by a vertical line, which is divided into coloured segments
 350 representing the membership coefficient to each genetic group, e.g. Mulhouse
 351 has 0.7 membership in cluster K3, 0.15 in K2, 0.1 in K1 and 0.05 in K5 (one colour
 352 per group). (A) STRUCTURE analysis including all (and only) individuals sampled
 353 in the OPSOs of Montpellier (K = 4). Numbers below the barplot correspond to the
 354 codes of the sampled OPSO. Groups of individuals sampled outdoors of OPSOs are
 355 indicated with a grey horizontal bar, while individuals sampled indoors are not.
 356 (B) STRUCTURE analysis including one individual by OPSO and by genetic group
 357 (with a red triangle indicating OPSO colonised by samples of several genetic
 358 groups) and (C) all individuals sampled in the various localities (K = 6). The
 359 STRUCTURE bar plots of the individuals from the OPSOs (B) and the localities (C)
 360 were produced in the same structure analysis. Individuals collected in OPSOs are
 361 not included in the map.

362 Focusing the analysis on the 9 OPSOs sampled in Montpellier, the most
 363 likely number of genetic clusters (K) detected for *T. darioi* was 4. However this
 364 clustering exhibited multimodality (*i.e.* different runs of STRUCTURE resulting
 365 in alternative distribution of individuals among clusters) with two modes (major
 366 mode with 10/15 runs). It remained the most likely (highest Evanno score) and
 367 other values of K also had multiple modes. Only a single cluster was detected
 368 in each OPSO, except for OPSO 21 where cluster 3 was detected indoor and
 369 cluster 3 and 4 outdoor (**Fig. 3A**). The broader analysis using *T. darioi* samples

370 from all localities (**Fig. 3C**) plus one individual per genetic cluster per
371 Montpellier OPSO as defined above, and individuals of other OPSOs (**Fig. 3B**)
372 suggested a most likely $K = 6$, despite exhibiting two modes (major mode with
373 14/15 runs).

374 The most common cluster in localities (K1, purple), especially along the
375 Spanish coast and outside the Mediterranean area, was detected in two OPSOs
376 in Montpellier and one in Lyon. The second most common cluster (K3, orange)
377 was found in Montpellier localities only (with a clustered distribution in the
378 South-West of the Montpellier area), and was detected in one Montpellier and
379 one Mulhouse OPSOs. The third most common cluster (K6, blue) distributed all
380 along the French Mediterranean coast localities was detected in one
381 Montpellier OPSO. The fourth most common cluster (K5, purple) was common
382 in Montpellier localities, and was detected in 3 Montpellier OPSOs. The fifth
383 most common cluster (K2, beige) present in Italy, Corsica and with a few
384 occurrences in Montpellier was not found in the sampled OPSOs. The less
385 common cluster (K4, green) was found in Montpellier localities only, and was
386 detected in 3 Montpellier OPSOs (**Fig. 3B, 3C**).



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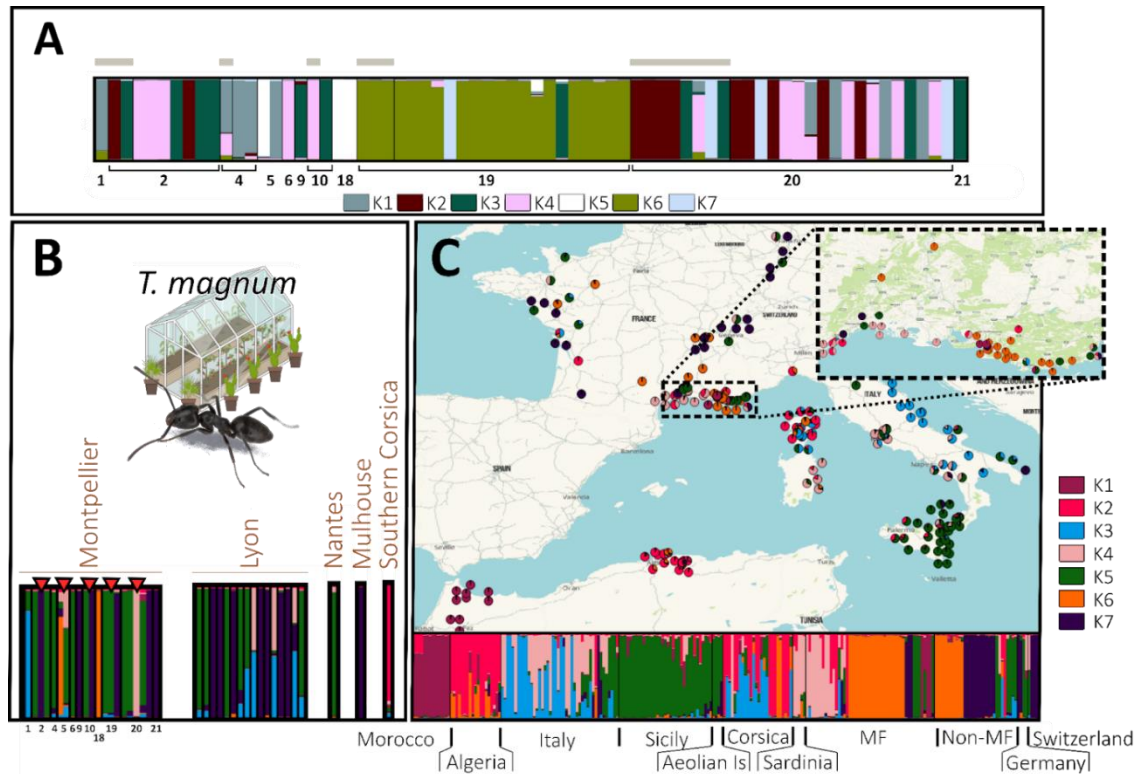
390 **Figure 4** - Population genetic structure of *T. ibericum*. In barplots, each
 391 individual is represented by a vertical line, which is divided into coloured
 392 segments representing the membership coefficient to each genetic group
 393 (one colour per group). **(A)** STRUCTURE analysis including all (and only)
 394 individuals sampled in the OPSOs of Montpellier ($K = 2$). Numbers below
 395 the barplot correspond to the codes of the sampled OPSO. Groups of
 396 individuals sampled outdoors the OPSOs are indicated with a grey
 397 horizontal bar, while individuals sampled indoors are not. **(B)** STRUCTURE
 398 analysis including one individual by OPSO and by genetic group (with a
 399 red triangle indicating OPSO colonised by samples of several genetic
 400 groups) and **(C)** all individuals sampled in the various localities, with S =
 401 South and N = North ($K = 3$). The STRUCTURE bar plots of the individuals
 402 from the OPSOs **(B)** and the localities **(C)** were produced in the same
 403 structure analysis. Individuals collected in OPSOs are not included in the
 404 map.

405 Focusing the analysis on the Montpellier OPSOs, the most likely number
 406 of genetic clusters detected for *T. ibericum* in the 5 OPSOs was 2; for this value
 407 of K there was only one mode. Only one single cluster was detected in each
 408 OPSO (**Fig. 4A**).

409 A broader analysis using samples from all localities (**Fig. 4C**) plus one
 410 individual per genetic cluster per Montpellier OPSO, and individuals of other
 411 OPSOs (**Fig. 4B**) suggested a most likely $K = 3$, despite exhibiting three modes
 412 (major mode with 9/15 runs).

413 The most common cluster in localities (K1, blue), especially in northern
 414 Spain, central Spain and Portugal, was detected in 3 Montpellier OPSOs. The
 415 second most common cluster (K3, orange) was found in southern Spain, and
 416 was detected in 2 Montpellier and 2 Lyon OPSOs (**Fig. 4B, 4C**).

417 3.5. Structure of *T. magnum* populations and putative source populations of
 418 OPSOs



419

420 **Figure 5** - Population genetic structure of *T. magnum*. In barplots, each
 421 individual is represented by a vertical line, which is divided into coloured
 422 segments representing membership coefficient to each genetic group
 423 (one colour per group). (**A**) STRUCTURE analysis including all (and only)
 424 individuals sampled in the OPSOs of Montpellier ($K = 7$). Numbers below
 425 the barplot correspond to the codes of the sampled OPSO. Groups of
 426 individuals sampled outdoors the OPSOs are indicated with a grey
 427 horizontal bar, while individuals sampled indoors are not. (**B**)
 428 STRUCTURE analysis including one individual by OPSO and by genetic group
 429 (with a red triangle indicating OPSO colonised by samples of several
 430 genetic groups) and (**C**) all individuals sampled in the various localities
 431 ($K = 7$). The STRUCTURE bar plots of the individuals from the OPSOs
 432 (**B**) and the localities (**C**) were produced in the same structure
 433 analysis and have the same cluster colour code. Individuals collected in
 434 OPSOs are not included in the map.

435 Focusing the analysis on the Montpellier OPSOs, the most likely number
 436 of genetic clusters detected for *T. magnum* in the 11 OPSOs was 7, for this
 437 K there was only one mode. In 5 out of 11 Montpellier OPSOs (OPSOs
 438 number 2, 5, 10, 19, 20), more than a single genetic group was identified
 439 (between 2 and 5 genetic groups). For the Montpellier OPSOs that included
 440 both indoor and outdoor samples, the number of genetic groups detected
 441 were generally higher indoors than outdoors. The genetic groups found in the outdoor

442 perimeter were detected in the indoor perimeter as well, except for OPSO
443 number 10, where samples found outdoors and indoors belonged to different
444 genetic groups (**Fig. 5A**).

445 A broader analysis using samples from all localities (**Fig. 5C**) plus one
446 individual per genetic cluster per Montpellier OPSO as defined above, and
447 individuals of other OPSOs (**Fig. 5B**) suggested a most likely $K = 7$, despite
448 exhibiting two modes (major mode with 9/15 runs).

449 Overall, clustering OPSOs with localities suggests diverse geographical
450 origins of ants found in OPSOs. All clusters found in putative native zones (*i.e.*
451 Italy, North Africa, clusters K1, K2, K3, K4, K5 and K7) were detected in OPSOs,
452 except for K1. Clusters K5 and K7, found in Sicily and south-eastern Italy
453 respectively, were highly prevalent in both OPSOs and non-Mediterranean
454 France localities. Cluster K6 was common in Mediterranean and non-
455 Mediterranean France, especially in Lyon, but only found in 2 OPSOs in
456 Montpellier. Most Algerian individuals had partial membership in this cluster,
457 suggesting a close relationship (**Fig. 5B, 5C**).

458 459 4. Discussion

460 In this study, we investigated the occurrence of three invasive species
461 of the *Tapinoma nigerrimum* complex within OPSOs in France, as well as the
462 role of OPSOs in their dissemination. Microsatellite markers were utilized to
463 identify *Tapinoma* species within OPSOs and to analyse their genetic structure.
464 This analysis involved worker samples from OPSOs in five French urban areas,
465 as well as from various locations in Europe and North Africa. Invasive
466 *Tapinoma*, most frequently *T. magnum*, were found in 37 over 101 OPSOs
467 inspected, supporting our main hypothesis that the trade in ornamental plants
468 plays a role in *Tapinoma* ants introductions in northern Europe. Additionally,
469 some of these OPSOs were colonised by several *Tapinoma* species
470 simultaneously. The potential source populations of the invasive *Tapinoma*
471 species found in the sampled OPSOs seem to be diverse for *T. magnum* and *T.*
472 *darioi*, indicating multiple geographic origins. Additionally, some OPSOs
473 housed multiple populations.

474 4.1. Spread dynamic of *Tapinoma* induced by OPSOs

475 We observed that *T. magnum*, *T. darioi* and *T. ibericum* are more
476 frequent in the OPSOs of Montpellier relative to the species regional
477 distribution revealed by the systematic sampling campaign of Centanni et al.
478 (2022) (which did not encompass OPSOs, but parks, streets...). Similarly, *T.*
479 *magnum* is common in Lyon OPSOs (16/61), but only 2 samples out of 1,248
480 sampling points were found during a systematic sampling in the area (Gippet
481 et al., 2017). This indicates a strong propagule pressure of *T. magnum* caused
482 by OPSOs. *Tapinoma darioi* and *T. ibericum* were less common in the Lyon
483 OPSO (1 and 2 occurrences respectively out of 61 OPSOs), but were not found
484 during systematic sampling in the locality (Gippet et al., 2017). Therefore,
485 OPSOs were potentially involved in the spread of *T. magnum*, *T. darioi* and *T.*
486 *ibericum* in several localities in France outside the Mediterranean zone.

487 In addition, we observed in Montpellier that when a genetic cluster was
488 present in the indoor perimeter of an OPSO for the three invasive species, it
489 was also found in the outdoor perimeter. This suggests that *Tapinoma* species

490 might be able to leave the buffered indoor conditions of OPSOs to forage in the
491 natural surrounding environment and potentially establish themselves after
492 being introduced through the plant trade. Alternatively, they could also
493 colonize indoor environments from outdoor ones. Indeed, invasive species of
494 the *Tapinoma nigerrimum* complex seem to be particularly flexible in terms of
495 environmental conditions, as shown in *T. magnum* which is able to rapidly
496 acclimate to new thermal conditions in a context of invasion (Bujan et al.,
497 2021).

498 *T. magnum* seems however to struggle to colonise Montpellier, despite
499 its ability to acclimatise to novel climatic conditions (Bujan et al., 2021). This
500 observation could result from niche and habitat saturation by sister species, in
501 particular *T. darioi* and *T. nigerrimum*. Destour et al., (2024) show that *T. darioi*
502 and *T. magnum* have similar temperature niches. In Montpellier, given the high
503 abundance of *T. darioi* (Centanni et al., 2022), the available niches could
504 potentially be saturated by this species, or other species native to the
505 Mediterranean region, which would be a competitor for *T. magnum*. This would
506 limit the spread of *T. magnum* in Montpellier, in the same way as species of
507 the *Tapinoma nigerrimum* complex could limit the spread of *L. humile* in
508 Corsica by competitive exclusion (Blight et al., 2010). In the case of the
509 *Tapinoma* species, this remains quite speculative at this stage. The differences
510 could also stem from varying introduction and invasion dynamics between the
511 two species.

512 In Montpellier OPSOs, we observed a relatively low number of
513 occurrences of *T. nigerrimum*, the species of the complex that is non-invasive
514 and native to this area. *Tapinoma nigerrimum* represents only 10.7% of the
515 occurrences of species of the *Tapinoma nigerrimum* complex in the OPSOs,
516 whereas in the Montpellier localities *T. nigerrimum* represents 70% of the
517 occurrences of species of the complex (Centanni et al., 2022). The low
518 occurrence of *T. nigerrimum* in the OPSOs may be due to its inability to form
519 supercolonies, reducing its chances of infecting soils and plants with a mated
520 queen capable of founding a new colony. In addition, in the OSPOs of its native
521 range, *T. nigerrimum* may be excluded by the other three species of the
522 complex after their introduction (Holway et al., 2002). In fact, a higher
523 proportion of the three invasive species of the *Tapinoma nigerrimum* complex
524 (*T. darioi*, *T. ibericum*, *T. magnum*) was observed in the Montpellier OPSOs
525 compared to the Montpellier localities. *T. nigerrimum* is also less abundant in
526 urbanised environments, where OPSOs are located (Centanni et al. 2022).
527 Given all these observations, we assume that the presence of *T. nigerrimum* in
528 OPSOs is most likely due to colonisation from the outdoors, while the presence
529 of *T. magnum* and *T. ibericum* is attributed to plant transport, and the presence
530 of *T. darioi* is probably due to both colonisation from the outdoors and plant
531 transport.

532 We were able to identify potential source populations for the ants found
533 in French OPSOs. The main localities hosting the potential source populations
534 of the invasive *Tapinoma* sampled in the nurseries are southern Italy for *T.*
535 *magnum* and Spain for *T. darioi* and *T. ibericum*. This aligns with the origins of
536 most plants in the Montpellier OPSOs (OPSOs staff, pers. comm.). These
537 findings support and further detail the hypothesis that the invasive *Tapinoma*
538 species found in western France originated from Spain and Italy, likely
539 introduced through plant pots from these regions (Gouraud & Kaufmann, 2022;
540 Lenoir et al., 2023). However, among the OPSOs sampled we also identified
541 populations of *T. darioi* probably originating from the south of France.

542 Nevertheless, inferring putative source populations does not account for non-
543 sampled populations. In our large-scale study, some populations may have
544 been missed due to their wide geographical distribution area. This can be
545 problematic if the non-sampled population acts as an invasion bridgehead
546 (Estoup & Guillemaud, 2010).

547 4.2. Multiple introductions at the population and species levels

548 Despite the fact that reproductive females have wings, natural dispersal
549 in the three invasive *Tapinoma* species seems limited to colony budding.
550 Species using this type of dispersal, as opposed to those using flight dispersal,
551 disperse over shorter distances (Cronin et al., 2013), which is incompatible with
552 the current distribution of the three species in Europe. Indeed, the dispersal
553 mode of these species should result in a high level of spatial genetic
554 structuration (Moffett, 2012). However, we observed that in *T. magnum* and *T.*
555 *darioi*, several genetic groups could be found within a single OPSO, indicating
556 a high frequency of long-distance transportation typical of human activities,
557 such as the transportation of ornamental plants. Hence, OPSOs could be
558 subjected to multiple introductions of different populations countering genetic
559 founder effects (Dlugosch & Parker, 2008; Zalewski et al., 2010). Multiple
560 introductions could therefore facilitate the establishment of invasive *Tapinoma*
561 populations at invaded sites by increasing genetic diversity, but also the
562 number of individuals and spatial range (Ahlroth et al., 2003; Roman & Darling,
563 2007). For instance, according to the estimations of Ross & Shoemaker,
564 (2008), the initial founding group of *Solenopsis invicta* colonising the USA
565 consisted of between 9 and 20 unrelated mated queens introduced in a city of
566 Alabama.

567 While detecting multiple introductions of *Tapinoma* populations, we
568 observed the presence of several invasive species from the *Tapinoma*
569 *nigerrimum* complex within individual OPSOs. The different species in this
570 complex can therefore get in close contact through the transport of ornamental
571 plants, which could lead these species to hybridise in the future, as suggested
572 by Seifert et al., (2017). Hybridisation is a phenomenon that can increase the
573 distribution areas of invasive species, in particular by increasing ecological
574 niche breadth (Pfennig et al., 2016; Carscadden et al., 2020). This phenomenon
575 could weaken the Allee effect responsible for failure of a large number of
576 biological invasions due to reduced individual fitness in small populations
577 (Yamaguchi, 2004; Mesgaran et al., 2016). Hybridization can also help to
578 increase fitness and invasive potential by improving biological traits such as
579 fertility (Schierenbeck & Ellstrand, 2009; Hovick & Whitney, 2014). For
580 example, in the invasive ant species *Solenopsis geminata* and *Solenopsis*
581 *xyloni*, hybrids show a competitive advantage over pure species, with hybrids
582 being more aggressive than *S. xyloni* and foraging more efficiently than *S.*
583 *geminata* (Axen et al., 2014). In species within the *Tapinoma nigerrimum*
584 complex, hybrids, as in *Solenopsis*, can produce fertile offspring (Fournier &
585 Aron, 2021). Therefore, we might also expect to find competitive advantages
586 in hybrids that would enhance their invasive characteristics (Seifert et al.,
587 2017; Fournier & Aron, 2021).

588 4.3. Management implications

589 Controlling the invasion routes and associated vectors remains the most
590 appropriate strategy for limiting biological invasions and mitigating their
591 effects (Hulme, 2009; Pergl et al., 2017). OPSOs make up the most visible part
592 of the global plant trade, but large landscaping operations such as new urban
593 green spaces import plants through bulk importers or directly from abroad. In
594 addition, invasive ants can be introduced through various other means such as
595 soil transport, food product shipment, or even vehicular transportation (Suhr
596 et al., 2019; Siddiqui et al., 2021; Hsu et al., 2024). The establishment of these
597 species in countries like the Netherlands, a global leader in the production and
598 export of ornamental plants, could result in worrying large scale secondary
599 spread and bridgehead effect (Van Tuyl, 2012; Javal et al., 2019; Blumenfeld
600 et al., 2021). Additionally, these species are thriving in anthropised habitats
601 such as urban areas (Centanni et al., 2022), which could potentially facilitate
602 their invasion of other similarly human-modified environments as suggested
603 by Hufbauer et al., (2012) («Anthropogenically Induced Adaptation to Invade»,
604 AIAI) and shown in the little fire ant, *Wasmannia auropunctata* (Foucaud et al.,
605 2013).

606 Monitoring OPSOs for invasive ant species could be part of routine
607 controls which are mandatory in Europe for some plant diseases and pests (e.g.
608 The Asian long-horned beetle *Anoplophora glabripennis*) (Commission
609 Delegated Regulation (EU), 2019). However, OPSOs staff lack the training,
610 financial resources, and technical capabilities to carry out invasive species
611 checks within their live plants. As a consequence, OPSOs and other centres of
612 exotic plant importation may serve as a pathway for many other invasive
613 species besides *Tapinoma* (Parrella et al., 2015; Blatrix et al., 2018). These
614 biological invasions can also have negative economic impacts on OPSOs,
615 adding to the urgency of addressing this issue (Parrella et al., 2015). Our
616 survey has revealed the presence of invasive *Tapinoma* ants in OPSOs of all
617 urban areas sampled. It would therefore be essential to allocate more
618 resources to government services dedicated to biological invasion issues.
619 Awareness-raising among national and European authorities, coupled with
620 support for OPSOs staff through training and funding, would be necessary for
621 effective management of these invasion routes (Cronin et al., 2017).

622

623 Conclusion

624 Overall, we reveal a pervasive and complex role of the ornamental plant
625 trade (most probably of trees requiring soil transport) in the human-mediated
626 continental and regional spread of three invasive ants of the *Tapinoma*
627 *nigerrimum* complex in western Europe. Using molecular markers, we linked
628 *Tapinoma* ants found in OPSOs to regions supplying ornamental plants, and
629 most strikingly, showed that there are multiple source populations being
630 introduced into OPSOs. However, our results also highlight that the presence
631 of invasive species in OPSOs does not always translate into the invasion of the
632 surrounding region. Indeed, although we documented high propagule pressure
633 of *Tapinoma magnum* in OPSOs in all studied French regions, in Montpellier,
634 where other species of the *Tapinoma nigerrimum* complex occur natively, this
635 invasive species was rare outside OPSOs. In contrast, outside the
636 mediterranean regions, where no *Tapinoma* of the *nigerrimum* complex occur

637 natively, invasive *T. magnum* populations were found outside OPSOs. This
638 research enhances our understanding of a significant invasion pathway for
639 ants and other invertebrates and stresses on the importance of collaborating
640 with OPSOs to prevent future introductions and limit ongoing ones.

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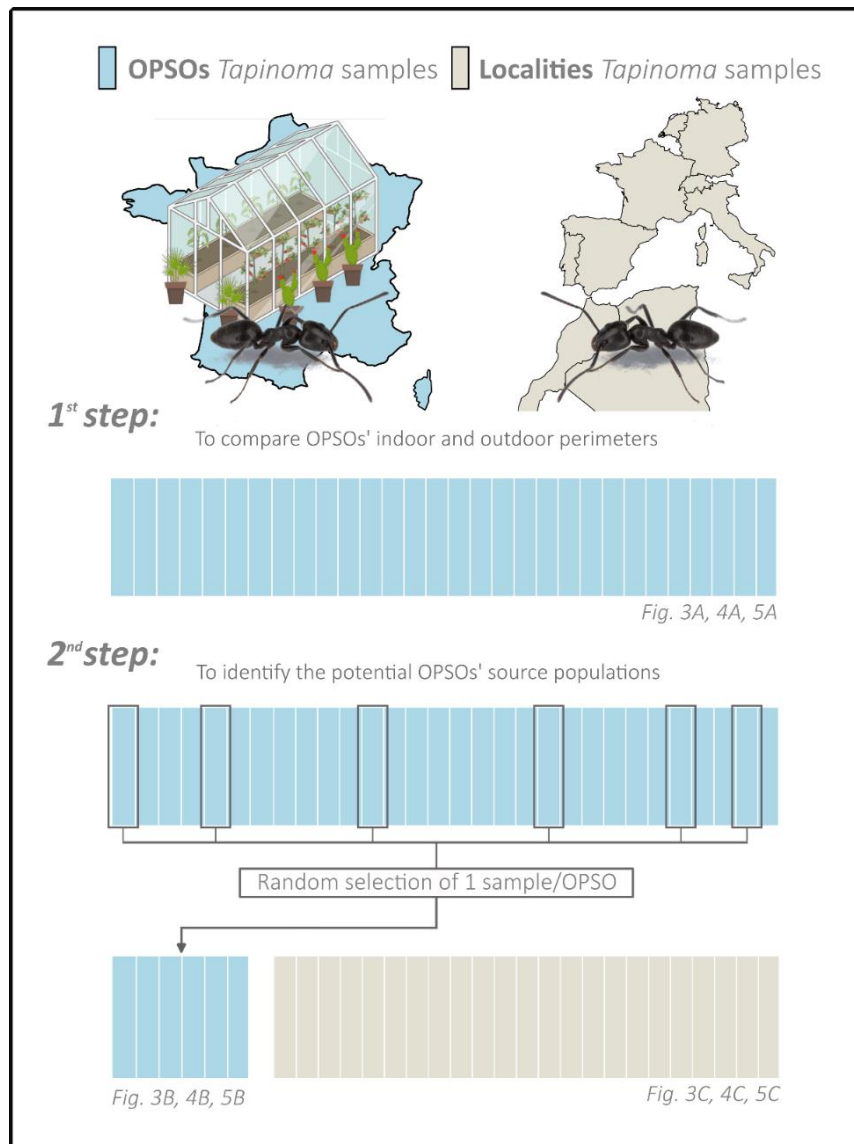
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Appendices



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Appendix 1 - Diagram of the two-step structure analysis conducted individually for the three *Tapinoma* species, along with the corresponding figure numbers in the results section. Each vertical line represents a hypothetical individual collected in a French OPSO (blue) or in localities (beige).

Outdoor perimeter	Indoor perimeter
<i>Aphaenogaster senilis</i> ; <i>Camponotus aethiops</i> ; <i>Camponotus piceus</i> ; <i>Cataglyphis piliscapa</i> ; <i>Crematogaster scutellaris</i> ; <i>Lasius cinereus</i> ; <i>Lasius</i> <i>niger</i> ; <i>Messor barbarus</i> ; <i>Messor ibericus</i> ; <i>Monomorium monomorium</i> ; <i>Myrmica spinosior</i> ; <i>Pheidole pallidula</i> ; <i>Plagiolepis pygmaea</i> ; <i>Tapinoma</i> <i>madeirense</i> ; <i>Temnothorax grp niger</i> ; <i>Temnothorax</i> <i>lichtensteini</i> ; <i>Temnothorax racovitzai</i> ; <i>Temnothorax</i> <i>recedens</i> ; <i>Temnothorax unifasciatus</i> ; <i>Tetramorium</i> <i>semilaeve</i>	<i>Aphaenogaster gibbosa</i> ; <i>Aphaenogaster senilis</i> ; <i>Camponotus</i> <i>aethiops</i> ; <i>Camponotus cruentatus</i> ; <i>Camponotus lateralis</i> ; <i>Cataglyphis piliscapa</i> ; <i>Crematogaster scutellaris</i> ; <i>Formica</i> <i>cunicularia</i> ; <i>Lasius cinereus</i> ; <i>Lasius grandis</i> ; <i>Lasius niger</i> ; <i>Messor ibericus</i> ; <i>Monomorium monomorium</i> ; <i>Myrmica spinosior</i> ; <i>Pheidole pallidula</i> ; <i>Plagiolepis pygmaea</i> ; <i>Tapinoma erraticum</i> ; <i>Tapinoma madeirense</i> ; <i>Temnothorax lichtensteini</i> ; <i>Temnothorax</i> <i>recedens</i> ; <i>Temnothorax unifasciatus</i> ; <i>Tetramorium grp</i> <i>caespitum</i> ; <i>Tetramorium semilaeve</i> ; <i>Tetramorium sp. 1</i> ; <i>Plagiolepis schmitzii</i> ; <i>Lasius neglectus</i>

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Appendix 2 - Ant species of Montpellier OPSOs depending sampling perimeter

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(A) OPSOs

Species	Region	Urban area	Sample date	n	OPSOs colonised
<i>T. darioi</i>	Occitanie	Montpellier	2023	111	9
	Auvergne-Rhone-Alpes	Lyon	2019	1	1
	Hauts-de-France	Mulhouse	2019	1	1
<i>T. ibericum</i>	Occitanie	Montpellier	2023	19	5
	Auvergne-Rhone-Alpes	Lyon	2019	2	2
<i>T. magnum</i>	Occitanie	Montpellier	2023	70	11
	Auvergne-Rhone-Alpes	Lyon	2019	16	16
	Hauts-de-France	Mulhouse	2019	1	1
	Pays de la Loire	Nantes	2020	1	1
	Corsica	Corsica	2021	1	1
<i>T. nigerrimum</i>	Occitanie	Montpellier	2023	11	3

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(B) Localities

Species	Locality	Region	Sample date	Latitude	Longitude	n
<i>T. darioi</i>	M-France	Provence-Alpes-Côte d'Azur	2019-2023	43.358053	5.354571	13
	M-France	Occitanie	2014-2023	43.664165	3.923175	119
	Italy	Lazio	2013-2014	41.886135,	12.392395	6
	Italy	Tuscany	2014	42.417	11.235	1
	Italy	Liguria	2014	44.149	9.685	1
	Corsica	Corsica	2012-2016	41.37359	9.18058	4
	NM-France	Borgogne -Franche-Comté	2016	46.7749512	4.8580844	1
	NM-France	Hauts-de-France	2019	49.20667	2.58578	1
	NM-France	Pays de la Loire	2019-2022	47.248001	-2.259574	4
	NM-France	Nouvelle-Aquitaine	2014	46.349727	-1.37036621	1
Switzerland	Vaud	2019	46.50557	6.65312	1	
<i>T. ibericum</i>	S-Portugal	Algarve	2016	37.07544	-8.75598	2
	N-Portugal	Norte	2013	41.551083	-7.146007	8
	S-Spain	Castilla-La Mancha	2012-2019	38.915170	-3.833179	4
	S-Spain	Region of Murcia	2017	38.345	-1.493	4
	S-Spain	Andalusia	2012-2023	37.331403	-3.570793	45
	N-Spain	Catalonia	-	42.44641983	1.78538584	3
	N-Spain	Community of Madrid	-	40.8672	-4.1003	1
	N-Spain	Asturias	2018	42.773069	-5.868145	1
	M-France	Occitanie	2019	43.42769	3.60826	1
	M-France	Provence-Alpes-Côte	2021-2023	43.644859	4.902519	3
Rotterdam	South Holland	2017	51.9585	4.5077	1	
<i>T. magnum</i>	Algeria	Bouria	-	36.4468505	3.9460482	11
	Algeria	Alger	-	36.742	3.1199497	8
	Morocco	Agmod	2014	35.158	-4.326	2
	Morocco	Tangier-Tetouan-Al Hoceima	2023	35.0985533	-5.27418667	5
	Morocco	Fas-Meknas	2023	33.91	-5.556	3
	Morocco	Sus-Massa	2014	31.51212	-9.76765	4
	Sicily	Sicily	2013-2018	37.387973	13.297286	35
	Aeolien is	Aeolien island	2014	38.57794	14.81013	4
	Italy	Apulia	2013	40.65	17.909	6
	Italy	Basilicata	2013	40.837	16.036	2
	Italy	Campania	2013	40.23079	14.9588	4
	Italy	Calabria	2013	39.925	15.756	1
	Italy	Abruzzo	2013	42.619	13.984	5
	Italy	Marche	2013-2014	42.88398	13.33942	4
	Italy	Tuscany	2017	43.765548	11.257823	1
	Italy	Liguria	2014	44.357	8.571	1
	Italy	Lazio	2013-2014	41.711056	12.36278	20
	Sardinia	Sardinia	2014	40.224633	9.625747	5
	Corsica	Corsica	2009-2021	42.0038	8.9201	26
	M-France	Provence-Alpes-Côte d'Azur	2014-2023	43.12076	5.93977	31
	M-France	Occitanie	2014-2021	43.446147	3.702157	16
	NM-France	Nouvelle-Aquitaine	2008-2022	45.519045	-1.122327	6
	NM-France	Pays de la Loire	2018-2022	48.136565	-1.6939176	7
	NM-France	Bretagne	2021	48.136565	-1.6939176	1
	NM-France	Normandie	2022	49.100326	-1.0791	1
	NM-France	Auvergne-Rhone-Alpes	2011-2023	45.741177	4.819881	15
	NM-France	Grand Est	2019	48.661742	7.611926	2
	Switzerland	Vaud	2017-2019	46.52156	6.64287	4
	Germany	Rhineland-Palatinate	2009-2012	49.263	8.135	4

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Appendix 3 - *Tapinoma* samples collected in (A) French OPSOs and (B) Western Europe and North Africa localities

664

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670

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675

Conflict of interest disclosure

676 The authors declare that they comply with the PCI rule of having no
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678

Data, scripts, code, and supplementary information availability

679

The Text uses the paragraph style "Text PCJ".

680

Data are available online: <https://doi.org/10.23708/V2AMCA>

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