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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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43 **ABSTRACT**

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

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

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1. Introduction

76 Understanding and preventing biological invasions is crucial because they are among
77 the leading causes of the ongoing biodiversity crisis, and threaten human health and societies
78 (McGeoch et al., 2010; Pyšek & Richardson, 2010; Diagne et al., 2021). Human activities, by
79 introducing species into new habitats, are the main cause of biological invasions globally (van
80 Kleunen et al., 2015; Bonnamour et al., 2021). Among the many species transported by humans
81 at global scale, some are able to establish and thrive in novel environments. They can
82 potentially spread beyond their initial introduction point and cause damages, and are referred
83 to as invasive alien species (Broennimann et al., 2007; Young et al., 2017; Pyšek et al., 2020;
84 Fenn-Moltu et al., 2023). Insects for instance, because of their small size, are easily
85 unintentionally transported by human activities through the contamination of traded materials
86 or by hitchhiking on vehicles (Meurisse et al., 2019; Gippet et al., 2019). Species can also become
87 invasive even within their native range by undergoing demographic explosions and rapidly
88 expanding into new areas, thereby creating significant challenges (Valéry et al., 2009).

89 Invasive ant species are highly destructive, causing harm not only to biodiversity but
90 also generating important socio-economic impacts (e.g. health issues, agricultural losses, costs
91 of control and eradication) (Lach & Thomas, 2008; Silverman & Brightwell, 2008; Siddiqui et al.,
92 2021; Tercel et al., 2023). For example, the fire ant *Solenopsis invicta* and the little fire ant
93 *Wasmannia auropunctata* have cost billions of USD in damages and control efforts in the last
94 decades (Angulo et al., 2022). Most invasive ant species can occupy various environments and
95 exploit a large quantity and diversity of resources within their new environments (Crowder &
96 Snyder, 2010; Felden et al., 2018; Balzani et al., 2021). Furthermore, these species often form
97 polygynous and polydomous (i.e. multiple-queen, multiple-nest) colonies, conducive to the
98 formation of supercolonies (Bertelsmeier et al., 2015; Helanterä, 2022). These supercolonies
99 expand through budding, a process by which queens (and some workers) establish new nests
100 close to the main colony while maintaining their connection to other nests by exchanging
101 workers and thus preserving social recognition within the entire supercolony (Torres et al.,
102 2007; Moffett, 2012; Helanterä, 2022). Supercolonies can cover large areas, with a high density
103 of workers exploiting available resources (Gippet et al., 2018). For example, some supercolonies
104 of *Lasius neglectus* can reach >20ha (Ugelvig et al., 2008; Gippet et al., 2022).

105 The *Tapinoma nigerrimum* complex comprises five ant species, *T. darioi*, *T. ibericum*, *T.*
106 *magnum*, *T. hispanicum* and *T. nigerrimum*, all of which originate from the Western
107 Mediterranean area (i.e. from Spain to Italy and Morocco to Tunisia). These species are very
108 similar morphologically and were considered to be a single species until the recent re-
109 evaluation of this complex and its subsequent revision (Seifert et al., 2017, 2024). This complex
110 comprises three polydomous species, which are capable of forming supercolonies (*T. darioi*, *T.*
111 *ibericum*, *T. magnum*), and two monodomous species (*T. nigerrimum* and *T. hispanicum*) (Seifert
112 et al., 2017, 2024). The three polydomous species have a great invasive potential as they can be
113 common in anthropised environments and appear to be spreading through human activities
114 (Seifert et al., 2017; Centanni et al., 2022; Lenoir et al., 2023). They also pose a threat to human
115 activities and to native ants (Mansour et al., 2012; Gippet, George, et al., 2022; Gouraud &
116 Kaufmann, 2022; Lenoir et al., 2023). *Tapinoma nigerrimum* and *T. hispanicum* which feature no
117 traits associated with invasiveness, can respectively be found in southern France/northern
118 Spain and southern/western Spain (Seifert et al., 2017, 2024). The probable native range of *T.*
119 *magnum* encompasses eastern and southern Italy and North Africa (Seifert et al., 2017; Gouraud
120 & Kaufmann, 2022). The situation in northern Italy and the Mediterranean coast of France is less
121 clear, but may be due to an earlier range expansion of *T. magnum* (Seifert et al., 2024).

122 *Tapinoma darioi* has a probable native distribution in North-East Spain and the French
123 Mediterranean coast. *Tapinoma ibericum* is found in the southern and western Iberian
124 peninsula including Spain and Portugal (Seifert et al., 2017; Gouraud & Kaufmann, 2022). In
125 addition, these three species have been introduced into northern Europe. The first proven
126 record for *T. magnum* out of its native range was in Edesheim, Germany in 2009 (Seifert et al.
127 2017) and the species is now present in Austria, Belgium, England, Germany, Switzerland and
128 the Netherlands. *Tapinoma darioi* was detected in the Netherlands and *T. ibericum* in England,
129 Germany and the Netherlands (Dekoninck et al., 2015; Seifert et al., 2017, 2024; Lenoir et al.,
130 2023). These species are also invasive in several Mediterranean and northern French localities,
131 where they exhibit invasive behaviour (Blight et al., 2010; Centanni et al., 2022; Gouraud &
132 Kaufmann, 2022; Lenoir et al., 2023). The three invasive species are present in different
133 proportions in the invaded areas, suggesting different patterns of introduction. In the urban
134 area of Montpellier (Mediterranean France), for example, Centanni et al., (2022) show a strong
135 abundance of *T. darioi* compared with the other two invasive species. On the other hand, in the
136 northern parts of France and Europe, *T. magnum* is the most common species (Seifert et al.,
137 2017; Lenoir et al., 2023).

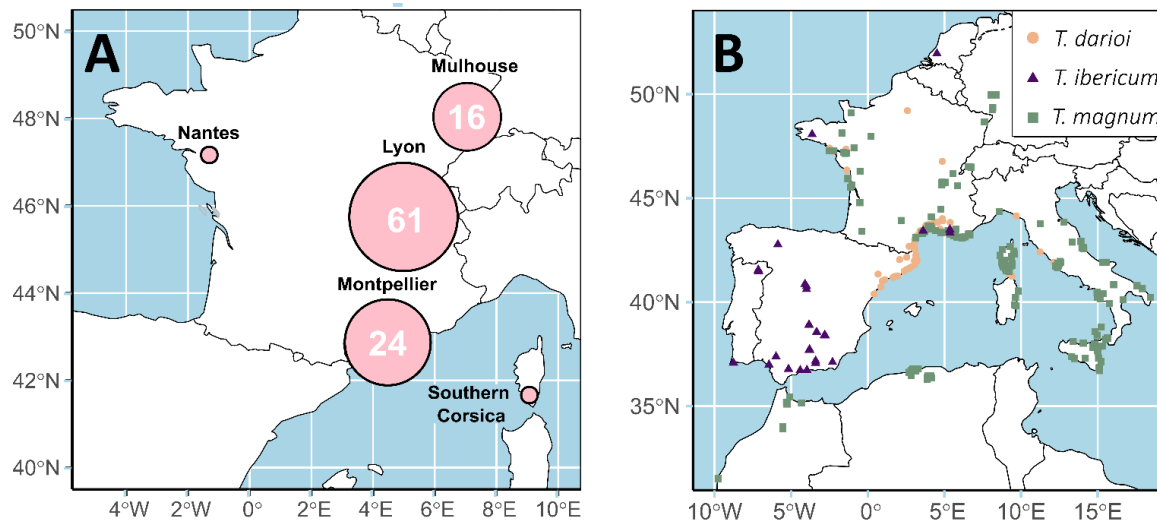
138 The European spread of invasive *Tapinoma* species is suspected to occur mostly
139 through the trade in ornamental plants (Seifert et al. 2024, Gouraud & Kaufmann, 2022). For
140 example, *Tapinoma* ants have been detected in pots of olive trees in Pays de la Loire (north-
141 west France) and Gironde (west France) departments (Gouraud & Kaufmann, 2022; Lenoir et al.,
142 2023). Yet, the role of the trade in ornamental plants in shaping ongoing invasions of *Tapinoma*
143 species remains unexplored. More generally, because it is still incipient, studying this invasion
144 could provide invaluable insights into one of the most common pathways for insect invasions.

145 In this study, we focused on the ongoing invasion of *T. darioi*, *T. ibericum* and *T. magnum*
146 in Western Europe. Our objective was to evaluate the role of Ornamental Plant Sales Outlets
147 (OPSOs) as an introduction pathway for ant invasions using genetic tools, with a particular
148 focus on the influx of species into OPSOs. We hypothesize that these species are more frequent
149 in OPSOs than in surrounding areas. We also expect OPSOs to host non-native populations and
150 act as hubs for invasion. To test these hypotheses, we collected and genotyped *Tapinoma*
151 workers from OPSOs located in four urban areas of metropolitan France and one locality in
152 Corsica with a specific focus on the Montpellier urban area (Mediterranean coast). We then
153 analysed their relationships to workers from a large number of localities of the distribution
154 range of the three species. This allowed us to determine species identity, define genetic groups
155 within species and infer the broad geographical origins of the *Tapinoma* ants found in OPSOs.

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2. Material and methods

2.1. Study sites and sampling



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Figure 1 - (A) Location of the French urban areas where OPSOs were sampled, with disk size proportional to the number of OPSOs collected (ranging from 1 (Nantes and Southern Corsica) to 61 depending on the urban area). (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 OPSOs in Nantes urban areas and southern Corsica were added to the dataset (**Fig. 1A**). The OPSOs were selected to represent a broad range of plant sellers (plant nurseries or garden centres). OPSO sampling was carried out by different teams of at least two people at different times of the day 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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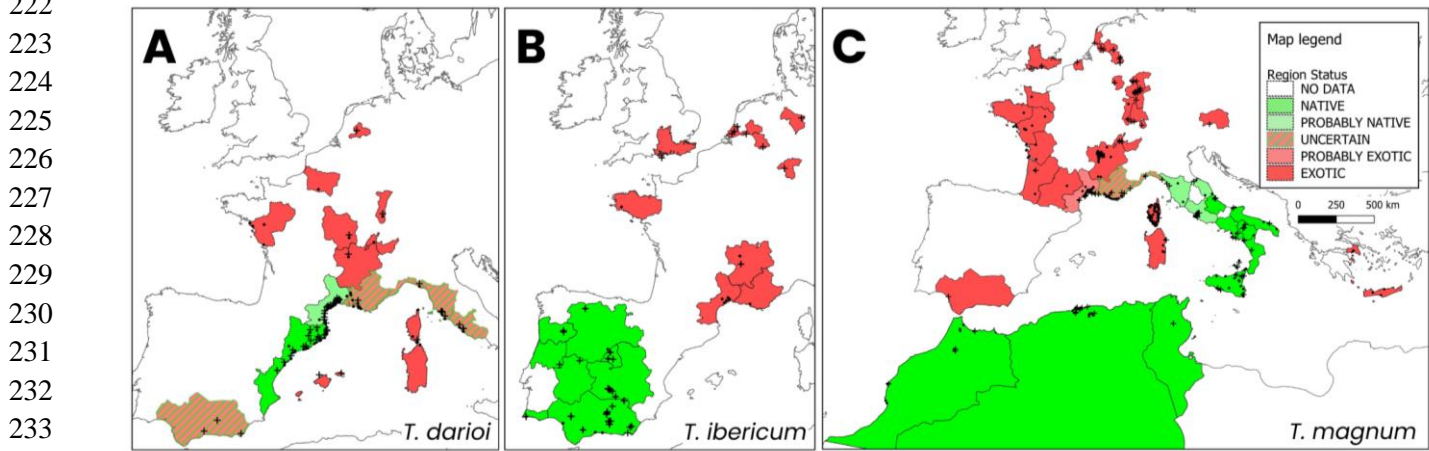
In the Lyon urban area (South of French continental bioregion) 61 OPSOs were sampled in spring 2019 and in the Mulhouse urban area (North of French continental bioregion) 16 OPSOs were sampled in summer 2019. The OPSOs were searched by visual prospection inside and outside, in all areas open to the public including greenhouses and open air plant nurseries. Only one *Tapinoma* sample was collected per OPSO in Lyon, regardless of the perimeter, but in Mulhouse, two samples were collected from the same OPSO: one indoors and one outdoors.

199 In the Nantes urban area (Oceanic bioregion) and southern Corsica (Mediterranean
200 Island), only one sample was collected by visual prospection in 1 OPSO in each urban area (**Fig.**
201 **1A**).

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

205 Data from Seifert et al., (2024), from the present article, and from records from Greece
206 (which were identified to species by genotyping but not used in the OPSO analysis) were used
207 to draw maps of the invasive status of *T. darioi*, *T. ibericum* and *T. magnum* in Europe and the
208 Mediterranean (**Fig. 2**, Appendix 1). Six categories were considered, based on the following
209 criteria:

- 210 ● NO DATA: no records in Seifert et al., (2024) or in the present study
- 211 ● NATIVE: distribution continuous, strong majority of records of the species compared to
212 other supercolonial *Tapinoma* species and Mediterranean plant export (i.e. export of
213 Mediterranean plants such as potted mature olive trees, which have been cited as
214 invasion vectors for the species group (Seifert et al., 2017))
- 215 ● PROBABLY NATIVE: at the edge of the continuous NATIVE distribution, Mediterranean
216 plant export but few records, some records of other supercolonial *Tapinoma* species
- 217 ● UNCERTAIN: at the edge of the continuous NATIVE distribution, Mediterranean plant
218 export but records of other supercolonial *Tapinoma* species are at least as frequent
- 219 ● PROBABLY EXOTIC: at the edge of continuous NATIVE distribution or discontinuous, with
220 a strong majority of records of other supercolonial *Tapinoma*
- 221 ● EXOTIC: distribution is discontinuous from the NATIVE distribution or not Mediterranean.



235 **Figure 2.** Maps of the known distribution and native/exotic status of (A) *T. darioi*, (B)
236 *T. ibericum* and (C) *T. magnum*. Crosses represent records from Seifert et al., (2024),
237 dots represent records which were identified by microsatellite genotyping in the
238 present study and in Greece. Crosses and dots overlap when records were both
239 genotyped and used in Seifert et al., (2024). Colors indicate native/exotic status of
240 European NUTs –level 2 regions, English regions and North-African countries. Bright
241 green indicates NATIVE status, muted green PROBABLY NATIVE, hatched green/red
242 UNCERTAIN status, muted red PROBABLY EXOTIC, bright red EXOTIC.

244 We used the NUTS 2024 layer for regional boundaries of continental Europe (NUTS level 2,
245 <https://ec.europa.eu/eurostat/web/gisco/geodata/statistical-units/territorial-units-statistics>),

246 the december 2023 regions layer for England (<https://geoportal.statistics.gov.uk/datasets>
247 [/regions-december-2023-boundaries-en-bfc-2/explore](https://geoportal.statistics.gov.uk/datasets/regions-december-2023-boundaries-en-bfc-2/explore)) and the World Administrative
248 Boundaries dataset for Algeria, Morocco and Tunisia
249 ([https://public.opendatasoft.com/explore/dataset/world-administrative-](https://public.opendatasoft.com/explore/dataset/world-administrative-boundaries/export/)
250 [boundaries/export/](https://public.opendatasoft.com/explore/dataset/world-administrative-boundaries/export/)).

251 All statuses are hypotheses based on our current knowledge of the distribution of
252 species. They might change with additional records and an in-depth population genetic
253 approach, which is outside the scope of the present article.

254 **2.2. DNA extraction and Genotyping**

255 DNA was extracted from workers of the *Tapinoma nigerrimum* complex collected from
256 OPSOs (n = 234) and from different localities (n = 486) by grinding each worker in proteinase K
257 (10 µL at 15 mg/ml) and Chelex 7% (150 µL). After grinding, samples were incubated at 55°C for
258 2 hours, followed by a further 15 minutes at 90°C to inactivate the proteinase K.

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

273 **2.3. Species identification and comparison of occurrences**

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

279 In the present study, an occurrence was defined as the presence of at least one
280 individual of a species in an OPSO or in one point of the standardised grid in Centanni et al.
281 (2022). We tested whether the proportion of occurrences of species of the *Tapinoma*
282 *nigerrimum* complex differed between outdoor and indoor perimeter of the OPSOs using
283 a χ^2 compliance test. We also tested if OPSOs samples were similar to samples from
284 Centanni et al. (2022) with an additional χ^2 .

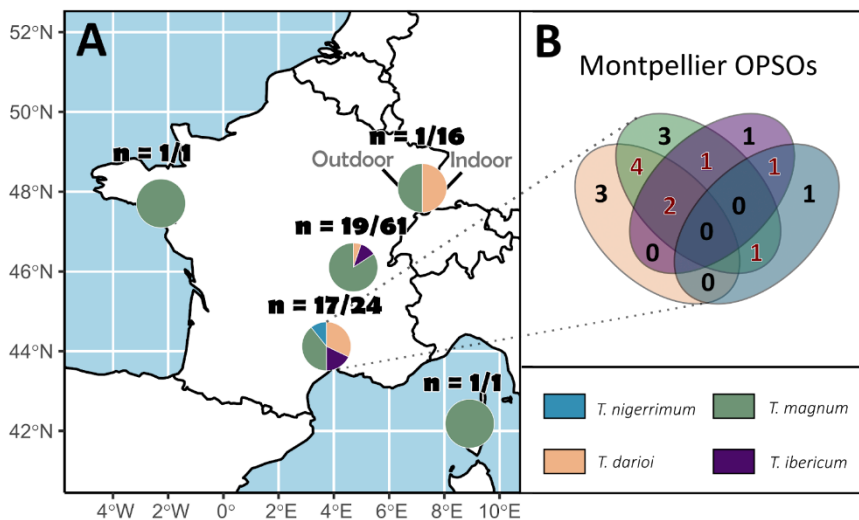
285 **2.4. Assessment of OPSOs population structure and identifying their source populations**

286 The genetic structure of the populations within each species was analysed by Bayesian
287 clustering using STRUCTURE 2.3.4 (Pritchard et al., 2000). Clustering analysis was realised in

288 two steps, consisting in a series of three analyses, one for each *Tapinoma* species (Appendix 2).
 289 Firstly, a STRUCTURE analysis was performed using only the OPSOs samples to determine
 290 whether there were one or more genetic groups within each OPSO and to know if the outdoor
 291 populations were the same as the indoor populations. Then, a second STRUCTURE analysis was
 292 performed in order to identify the potential source populations of the OPSOs. For this second
 293 step, we used a dataset consisting of samples from various localities in Western Europe and
 294 North Africa. This dataset included either 179 samples of *T. darioi* species, 234 samples of *T.*
 295 *magnum* species, or 30 samples of *T. ibericum* species, which served as the reference source
 296 populations. We included one individual (selected randomly) per genetic group and per OPSO,
 297 which were the specimens whose origin was to be determined. Not all specimens from OPSOs
 298 were used to avoid potential bias in Bayesian analysis. For each STRUCTURE analysis, an
 299 admixture model was built using a burn-in period of 250,000 iterations, followed by 250,000
 300 MCMC (Markov Chain Monte Carlo) iterations. For each potential number of genetic groups,
 301 denoted as K (ranging from 1 to 10) (Pritchard et al., 2000), a total of 15 independent runs
 302 were executed. For each STRUCTURE analyses the K values were selected using three
 303 criteria : high Evanno's ΔK (Earl & vonHoldt, 2012), high mean similarity between the runs and
 304 small number of minor clusters. The admixture models obtained from these analyses were then
 305 compiled using CLUMPAK (Kopelman et al., 2015) which provides consensus between similar
 306 runs generated by STRUCTURE. The spatial distribution of genotypes for samples from the
 307 various localities was then mapped out using QGIS 3.28.3, using the compilation of the runs
 308 from STRUCTURE built in CLUMPAK during the second analysis.

3. Results

3.1. Occurrences of *Tapinoma* species in OPSOs



313 **Figure 3 - (A)** Proportion of occurrences of *Tapinoma nigerrimum* complex species in
 314 French OPSOs (n = number of OPSOs colonised / total number of OPSOs visited) **(B)** Venn
 315 diagram showing occurrences (black numbers) and co-occurrences (red numbers) of *T.*
 316 *magnum*, *T. darioi* and *T. ibericum* in 17 Montpellier OPSOs (in the other areas only one
 317 sample was collected per OPSO, and thus, co-occurrences could not be investigated).
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320 An important proportion of OPSOs featured *Tapinoma* species (37.8%). Where
321 systematic sampling was carried out, the presence of *Tapinoma* species in OPSOs varied
322 strongly depending on urban areas: 70.8% in Montpellier; 31.1% in Lyon; 6.3% in Mulhouse.
323 Over the 103 sampled OPSOs, *T. magnum* was the most frequently found with 30 occurrences
324 (29.1%), *T. darioi* was found in 11 OPSOs (10.7%), *T. ibericum* in 7 OPSOs (6.8%) and *T.*
325 *nigerrimum* 3 OPSOs (2.9%) (Fig. 3A).

326 3.2. Occupancy of baits by *Tapinoma* species in Montpellier

327 Among the baits of 24 OPSOs in Montpellier, an average of 5.5 baits out of 20 were visited
328 by ants indoors, and 6.5/20 outdoors. Among these baits, a total of 30 species were collected,
329 with 26 species indoors and 20 species outdoors (Appendix 3). Among these 30 species, two
330 were unambiguously exotic: *Plagiolepis schmitzii* and *Lasius neglectus*. These two species were
331 present in only 1% of the occupied baits. Species of the *Tapinoma nigerrimum* complex were
332 found on 14.8% of the occupied baits, while other species occupied 85.2% of the baits. The
333 majority of *Tapinoma nigerrimum* complex workers collected for the study were sampled
334 through active prospection (78%).

335 3.3. Occurrences of *Tapinoma* species in Montpellier and Lyon

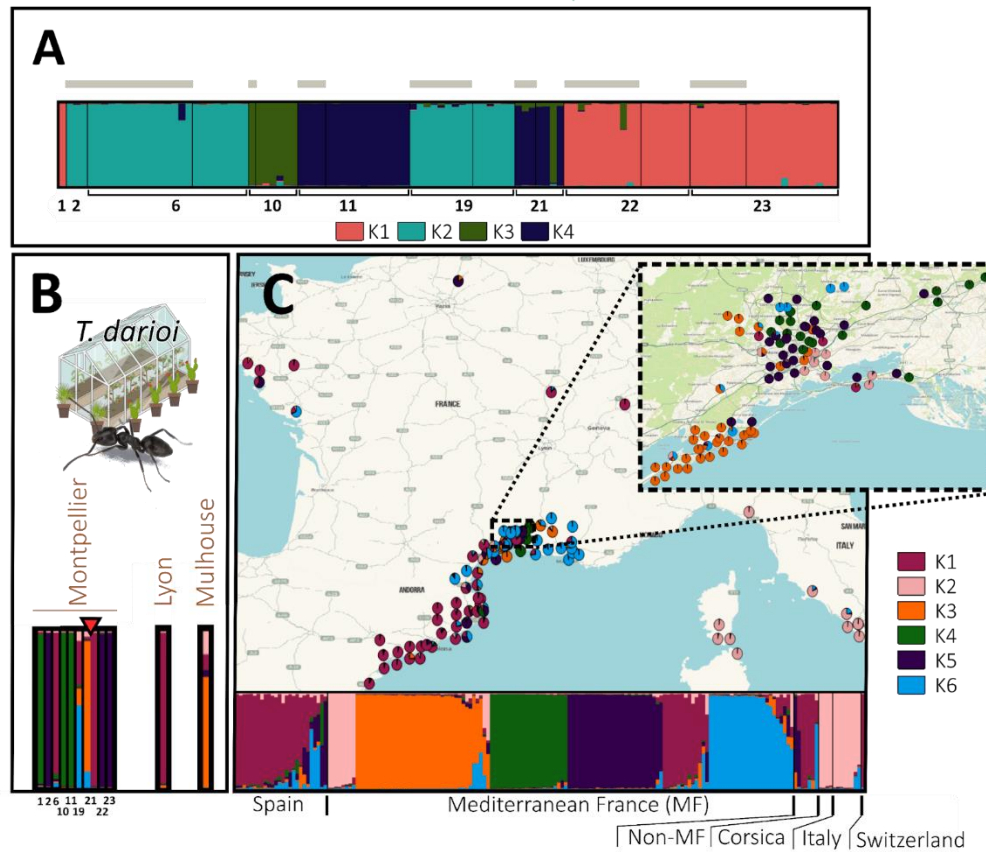
336 Seven OPSOs were colonised simultaneously by more than one invasive *Tapinoma*
337 species: 2 by *T. darioi*, *T. ibericum* and *T. magnum*, 4 by *T. darioi* and *T. magnum* and 1 by *T.*
338 *ibericum* and *T. magnum*. *Tapinoma nigerrimum* was also found co-occurring, once with *T.*
339 *ibericum* and once with *T. darioi*. (Fig. 3B). The indoor perimeters of 17/24 OPSOs were
340 colonised by at least one species from the *Tapinoma nigerrimum* complex. In the 24 OPSOs,
341 there were 8 occurrences (one occurrence = at least one individual of one species regardless of
342 the sampling method in one OPSO) of *T. darioi* (32%), 5 occurrences of *T. ibericum* (20%), 10
343 occurrences of *T. magnum* (40%), and 2 occurrences of *T. nigerrimum* (8%). The outdoor
344 perimeter of 14/24 OPSOs presented at least one *Tapinoma nigerrimum* complex species: 8
345 occurrences of *T. darioi* (47%), 1 occurrence of *T. ibericum* (5.9%), 6 occurrences of *T. magnum*
346 (35.3%), and 2 occurrences of *T. nigerrimum* (11.8%). The relative proportions of the four
347 species discovered in the indoor and outdoor perimeter OPSOs did not differ significantly
348 ($\chi = 0.41$, $P = 0.82$). In the Montpellier OPSOs a total of 211 workers of the *Tapinoma*
349 *nigerrimum* complex were genotyped, consisting of 111 *T. darioi*, 19 *T. ibericum*, 70 *T. magnum*
350 used for STRUCTURE analysis (1 individual corresponding to 1 bar) and 11 *T. nigerrimum*
351 (Appendix 1).

352 In contrast, in the localities of Montpellier (not taking into account OPSOs sampling), for
353 926 sampling point, occurrences were as follows: 78 *T. darioi* (27.8%), 1 *T. ibericum* (0.3%), 6 *T.*
354 *magnum* (2.1%) and 197 *T. nigerrimum* (69.8%) (Centanni et al., 2022). The relative proportions
355 of the four species discovered in the indoor and outdoor perimeter OPSOs differed
356 significantly from those sampled in Montpellier localities ($\chi = 20.32$, $P = 0.00004$ for indoors
357 and $\chi = 6.90$, $P = 0.03$ for outdoors). The proportion of *T. magnum*, *T. darioi* and *T. ibericum* is
358 higher than expected, while the number of *T. nigerrimum* is lower than expected in OPSOs.

359 In the 31.1% OPSOs colonised in Lyon, there were 1 occurrence of *T. darioi*, 2
360 occurrences of *T. ibericum* and 16 occurrences of *T. magnum*. In the localities of Lyon (not taking
361 into account OPSOs sampling), for 1248 sampling points, occurrences were as follows : 0 *T.*
362 *darioi*, 0 *T. ibericum*, 2 *T. magnum* (unpublished data from Gippet et al., 2017).

363

3.4. Structure of *Tapinoma darioi* populations and putative source populations of OPSOs



365

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

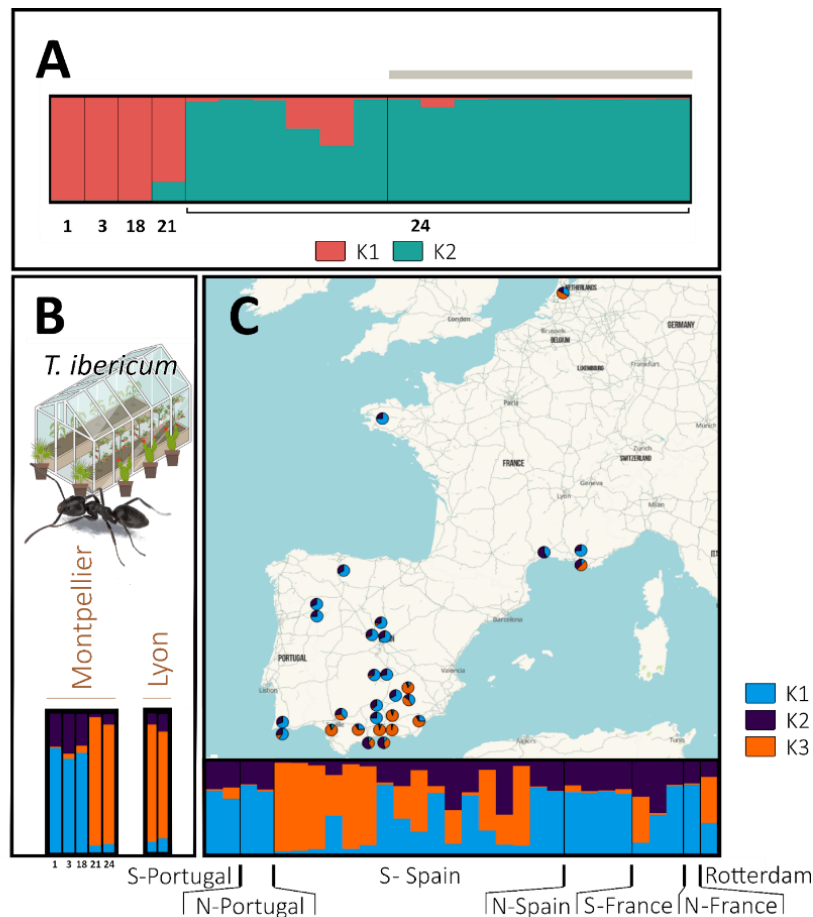
Focusing the analysis on the 9 OPSOs sampled in Montpellier, the most likely number of genetic clusters (K) detected for *T. darioi* was 4. However this clustering exhibited multimodality (*i.e.* different runs of STRUCTURE resulting in alternative distribution of individuals among clusters) with two modes (major mode with 10/15 runs). It remained the most likely (highest Evanno score) and other values of K also had multiple modes. Only a single cluster was detected in each OPSO, except for OPSO 21 where cluster 3 was detected outdoor and cluster 3 and 4 indoor (**Fig. 4A**). The broader analysis using *T. darioi* samples from all localities (**Fig. 4C**) plus one individual per genetic cluster per Montpellier OPSO as defined above, and individuals of other OPSOs (**Fig. 4B**) suggested a most likely K = 6, despite exhibiting two modes (major mode with 14/15 runs).

The most common cluster in localities (K1, light purple, **Fig. 4C**), especially along the Spanish coast and outside the Mediterranean area, was detected in two OPSOs in Montpellier and one in Lyon. The second most common cluster (K3, orange, **Fig. 4C**) was found in

369

390 Montpellier localities only (with a clustered distribution in the South-West of the Montpellier
 391 area), and was detected in one Montpellier and one Mulhouse OPSO. The third most common
 392 cluster (K6, blue) distributed all along the French Mediterranean coast localities was detected
 393 in one Montpellier OPSO. The fourth most common cluster (K5, dark purple, **Fig. 4C**) was
 394 common in Montpellier localities, and was detected in 3 Montpellier OPSOs. The fifth most
 395 common cluster (K2, beige) present in Italy, Corsica and with a few occurrences in Montpellier
 396 was not found in the sampled OPSOs. The less common cluster (K4, green) was found in
 397 Montpellier localities only, and was detected in 3 Montpellier OPSOs (**Fig.4B, 4C**).

398
 399 **3.5. Structure of *Tapinoma ibericum* populations and putative source populations of**
 400 **OPSOs**



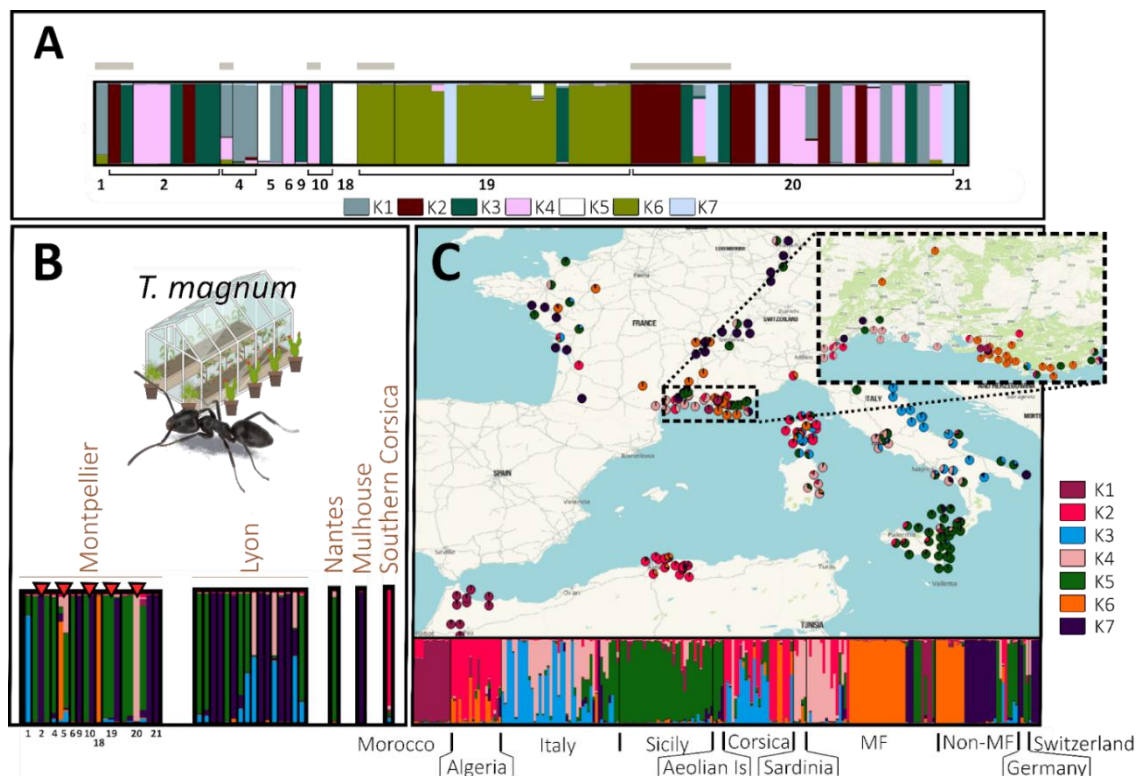
401
 402 **Figure 5** - Population genetic structure of *T. ibericum*. In barplots, each individual is
 403 represented by a vertical line, which is divided into coloured segments representing the
 404 membership coefficient to each genetic group (one colour per group). **(A)** STRUCTURE
 405 analysis including all individuals sampled in the OPSOs of Montpellier (K = 2). Numbers
 406 below the barplot correspond to the codes of the sampled OPSO. Individuals sampled
 407 outdoors the OPSOs are indicated with a grey horizontal bar, while individuals sampled
 408 indoors are not. **(B)** STRUCTURE analysis including one individual by OPSO and by
 409 genetic group and **(C)** all individuals sampled in the various localities, with S = South and
 410 N = North (K = 3). The STRUCTURE bar plots of the individuals from the OPSOs **(B)** and the
 411 localities **(C)** were produced in the same structure analysis. Individuals collected in
 412 OPSOs are not included in the map.

413 Focusing the analysis on the Montpellier OPSOs, the most likely number of genetic
 414 clusters detected for *T. ibericum* in the 5 OPSOs was 2; for this value of K there was only one

415 mode. Only one single cluster was detected in each OPSO (**Fig. 5A**). A broader analysis using
 416 samples from all localities (**Fig. 5C**) plus one individual per genetic cluster per Montpellier
 417 OPSO, and individuals of other OPSOs (**Fig. 5B**) suggested a most likely $K = 3$, despite exhibiting
 418 three modes (major mode with 9/15 runs).

419 The most common cluster in localities (K1, blue, **Fig. 5C**), especially in northern Spain,
 420 central Spain and Portugal, was detected in 3 Montpellier OPSOs. The second most common
 421 cluster (K3, orange) was found in southern Spain, and was detected in 2 Montpellier and 2 Lyon
 422 OPSOs (**Fig. 5B, 5C**).

423 **3.6. Structure of *Tapinoma magnum* populations and putative source populations of**
 424 **OPSOs**



425

426 **Figure 6** - Population genetic structure of *T. magnum*. In barplots, each individual is
 427 represented by a vertical line, which is divided into coloured segments representing
 428 membership coefficient to each genetic group (one colour per group). (A) STRUCTURE
 429 analysis including all individuals sampled in the OPSOs of Montpellier ($K = 7$). Numbers
 430 below the barplot correspond to the codes of the sampled OPSO. Individuals sampled
 431 outdoors the OPSOs are indicated with a grey horizontal bar, while individuals sampled
 432 indoors are not. (B) STRUCTURE analysis including one individual by OPSO and by
 433 genetic group (with a red triangle indicating OPSO colonised by samples of several
 434 genetic groups) and (C) all individuals sampled in the various localities ($K = 7$). The
 435 STRUCTURE bar plots of the individuals from the OPSOs (B) and the localities (C) were
 436 produced in the same structure analysis and have the same cluster colour code.
 437 Individuals collected in OPSOs are not included in the map.

438 Focusing the analysis on the Montpellier OPSOs, the most likely number of genetic
 439 clusters detected for *T. magnum* in the 11 OPSOs was 7, for this K there was only one mode. In
 440 5 out of 11 Montpellier OPSOs (OPSOs number 2, 5, 10, 19, 20), more than a single genetic group
 441 was identified (between 2 and 5 genetic groups). For the Montpellier OPSOs, the number of

442 genetic groups detected were generally higher indoor than outdoor. The genetic groups found
443 in the outdoor perimeter were detected in the indoor perimeter as well, except for OPSO
444 number 10, where samples found outdoor and indoor belonged to different genetic groups
445 (Fig. 6A).

446 A broader analysis using samples from all localities (Fig. 6C) plus one individual per
447 genetic cluster per Montpellier OPSO as defined above, and individuals of other OPSOs (Fig.
448 6B) suggested a most likely $K = 7$, despite exhibiting two modes (major mode with 9/15 runs).

449 Overall, clustering OPSOs with localities suggests diverse geographical origins of ants found
450 in OPSOs. All clusters found in putative native zones (*i.e.* Italy, North Africa, clusters K1, K2, K3,
451 K4, K5 and K7) were detected in OPSOs, except for K1. Clusters K5 and K7, found in Sicily and
452 south-eastern Italy respectively, were highly prevalent in both OPSOs and non-Mediterranean
453 France localities. Cluster K6 was common in Mediterranean and non-Mediterranean France,
454 especially in Lyon, but only found in 2 OPSOs in Montpellier. Most Algerian individuals had
455 partial membership in this cluster, suggesting a close relationship (Fig. 6B, 6C).

456
457

4. Discussion

458 In this study, we investigated the occurrence of three invasive species of the *Tapinoma*
459 *nigerrimum* complex within OPSOs in Mediterranean and non-Mediterranean French areas, as
460 well as the role of OPSOs in their introduction into new localities. Microsatellite markers were
461 utilised to identify *Tapinoma* species within OPSOs and to analyse their genetic structure. This
462 analysis involved worker samples from OPSOs in four urban areas of metropolitan France and
463 one locality in Corsica, as well as from various locations in Europe and North Africa. Invasive
464 *Tapinoma*, most frequently *T. magnum*, were found in 37 out of 101 OPSOs inspected,
465 supporting the hypothesis that the ornamental plant trade could play a role as a hub for the
466 introduction of *Tapinoma* ants in France. Additionally, some of these OPSOs were colonised by
467 several *Tapinoma* species simultaneously. The potential source populations of the invasive
468 *Tapinoma* species found in the sampled OPSOs seem to be diverse for *T. magnum* and *T. darioi*,
469 indicating multiple geographic origins. Additionally, some OPSOs housed multiple populations
470 of the same species.

4.1. Spread dynamic of *Tapinoma* induced by OPSOs

471
472 First of all, we observed that the percentage of colonised OPSOs and the presence of
473 invasive *Tapinoma* species differ across cities, with a high percentage in Montpellier, an
474 intermediate level in Lyon, and a low percentage in Mulhouse. This difference could be
475 explained by the introduction of material from the native regions of these species. In particular,
476 Montpellier probably imports more Mediterranean plants than Mulhouse due to geographic
477 proximity and climatic similarity, and thus, has a higher probability of introducing *Tapinoma*.
478 Additionally, we can assume that the climate in Mulhouse is less favorable for *Tapinoma*, which
479 are Mediterranean species (Seifert et al. 2024), making their maintenance in and around OPSOs
480 more challenging. Nonetheless, the sampling of Mulhouse OPSO was conducted during the
481 summer, a period when *Tapinoma* is less active than in spring (Destour et al., 2024).
482 Consequently, we likely underestimated the presence of *Tapinoma* in this locality.

483 We observed that *T. magnum*, *T. darioi* and *T. ibericum* are more frequent in the OPSOs
484 of Montpellier relative to the respective species regional distribution revealed by the systematic
485 sampling campaign of Centanni et al. (2022) (which did not encompass OPSOs, but urban

486 environments such as parks or streets). Similarly, *T. magnum* is common in Lyon OPSOs (16/61),
487 but only 2 samples out of 1,248 sampling points were found during a systematic sampling in the
488 area (Gippet et al., 2017). This indicates a strong propagule pressure of *T. magnum* caused by
489 OPSOs. *Tapinoma darioi* and *T. ibericum* were less common in the Lyon OPSOs (1 and 2
490 occurrences respectively out of 61 OPSOs), but were not found during systematic sampling in
491 the locality (Gippet et al., 2017). Therefore, OPSOs were potentially involved in the spread of *T.*
492 *magnum*, *T. darioi* and *T. ibericum* in several localities in France outside the Mediterranean
493 zone. Nonetheless, we should consider that there is a significant time gap between the
494 sampling of the Montpellier and Lyon OPSOs and the surrounding localities, with the OPSOs
495 sampled later in both cases. The expansion of invasive ants can occur rapidly, as demonstrated
496 by *Lasius emarginatus* in New York (Kennett et al., 2024), where noticeable spread took place
497 within just a few years. Therefore, the observed difference in frequency between invasive
498 *Tapinoma* species in OPSOs and surrounding localities may be partly explained by this
499 temporal gap, where an overall increase in frequency in both areas over time could lead to an
500 apparent overrepresentation in OPSOs.

501 In Montpellier we observed that when a genetic cluster was present in the indoor
502 perimeter of an OPSO for the three invasive species, it was also found in the outdoor perimeter.
503 This suggests that *Tapinoma* species might be able to leave the buffered indoor conditions of
504 OPSOs to forage in the natural surrounding environment and potentially establish themselves
505 after being introduced through the plant trade. Alternatively, they could also colonize indoor
506 environments from outdoor ones. Indeed, invasive species of the *Tapinoma nigerrimum*
507 complex seem to be particularly flexible in terms of environmental conditions, as shown in *T.*
508 *magnum* which is able to rapidly acclimate to new thermal conditions in a context of invasion
509 (Bujan et al., 2021).

510 *Tapinoma magnum* seems however to struggle to colonise the Montpellier region,
511 despite its ability to acclimatise to novel climatic conditions (Bujan et al., 2021). This
512 observation could result from niche and habitat saturation by sister species, in particular *T.*
513 *darioi* and *T. nigerrimum*. Destour et al., (2024) showed that *T. darioi* and *T. magnum* forage at
514 similar temperatures. In Montpellier, given the high abundance of *T. darioi* (Centanni et al.,
515 2022), the available niches could potentially be saturated by this species, or other species
516 native to the Mediterranean region, which would be a competitor for *T. magnum*. This would
517 limit the spread of *T. magnum* in Montpellier, in the same way as species of the *Tapinoma*
518 *nigerrimum* complex could limit the spread of *L. humile* in Corsica by competitive exclusion
519 (Blight et al., 2010). In the case of the *Tapinoma* species, this remains quite speculative at this
520 stage. The differences could also stem from varying introduction and invasion dynamics
521 between the two species.

522 In Montpellier OPSOs, we observed a relatively low number of occurrences of *T.*
523 *nigerrimum*, the species of the complex that is non-invasive and native to this area. *Tapinoma*
524 *nigerrimum* represents only 10.7% of the occurrences of species of the *Tapinoma nigerrimum*
525 complex in the OPSOs, whereas in the Montpellier localities *T. nigerrimum* represents 70% of
526 the occurrences of species of the complex (Centanni et al., 2022). The low occurrence of *T.*
527 *nigerrimum* in the OPSOs may be due to its inability to form supercolonies, reducing its chances
528 of infecting soils and plants with a mated queen capable of founding a new colony. In addition,
529 in the OPSOs of its native range, *T. nigerrimum* may be excluded by the other three species of
530 the complex after their introduction (Holway et al., 2002). In fact, a higher proportion of the
531 three invasive species of the *Tapinoma nigerrimum* complex (*T. darioi*, *T. ibericum*, *T. magnum*)
532 was observed in the Montpellier OPSOs compared to the Montpellier localities. *T. nigerrimum* is
533 also less abundant in urbanised environments, where OPSOs are located (Centanni et al. 2022).

534 Given all these observations, we assume that the presence of *T. nigerrimum* in OPSOs is most
535 likely due to colonisation from the outdoors, while the presence of *T. magnum* and *T. ibericum*
536 is attributed to plant transport, and the presence of *T. darioi* is probably due to both
537 colonisation from the outdoors and plant transport.

538 We were able to identify potential source populations for the ants found in French
539 OPSOs. The main localities hosting the potential source populations of the invasive *Tapinoma*
540 sampled in the OPSOs are southern Italy for *T. magnum* and Spain for *T. darioi* and *T. ibericum*.
541 This aligns with the origins of most plants in the Montpellier OPSOs (OPSOs staff, pers. comm.).
542 These findings support and further detail the hypothesis that the invasive *Tapinoma* species
543 found in western France originated from Spain and Italy, likely introduced through plant pots
544 from these regions (Gouraud & Kaufmann, 2022; Lenoir et al., 2023). However, among the
545 OPSOs sampled, we also identified populations of *T. darioi* and *T. magnum*, which are probably
546 originating from the south of France, since their genetic clusters have been found only in
547 southern France. Nevertheless, inferring putative source populations does not account for non-
548 sampled populations. In our large-scale study, some populations may have been missed due to
549 their wide geographical distribution area. This can be problematic if the non-sampled
550 population acts as an invasion bridgehead (Estoup & Guillemaud, 2010).

551 **4.2. Multiple introductions at the population and species levels**

552 Despite having wings, the natural dispersal of supercolonial *Tapinoma* mated gynes
553 usually takes place close to the home colony, where they seek adoption in conspecific nests
554 (Seifert et al. 2024). Species using this type of dispersal, as opposed to those using mainly flight
555 dispersal, disperse over shorter distances (Cronin et al., 2013), which is incompatible with the
556 current distribution of the three species in Europe. Indeed, the dispersal mode of these species
557 should result in a high level of spatial genetic structuration (Moffett, 2012). However, we
558 observed that in *T. magnum* and *T. darioi*, several genetic groups could be found within a single
559 OPSO, indicating a high frequency of long-distance transportation typical of human activities,
560 such as the transportation of ornamental plants. Hence, OPSOs could be subjected to multiple
561 introductions of different populations countering genetic founder effects (Dlugosch & Parker,
562 2008; Zalewski et al., 2010). Multiple introductions could therefore facilitate the establishment
563 of invasive *Tapinoma* populations at invaded sites by increasing genetic diversity, as well as
564 propagule pressure and spatial range (Ahlroth et al., 2003; Roman & Darling, 2007). A striking
565 example of this process is the case of *Solenopsis invicta* in the USA, whose initial founding group
566 colonizing the country is estimated to have consisted of only 9 to 20 unrelated mated queens
567 introduced into a city in Alabama (Ross & Shoemaker, 2008).

568 While detecting multiple introductions of *Tapinoma* populations, we observed the
569 presence of several invasive species from the *Tapinoma nigerrimum* complex within individual
570 OPSOs. The different species in this complex can therefore get in close contact through the
571 transport of ornamental plants, which could lead these species to hybridise in the future, as
572 suggested by Seifert et al., (2017). Hybridisation is a phenomenon that can increase the
573 distribution areas of invasive species, in particular by increasing ecological niche breadth
574 (Pfennig et al., 2016; Carscadden et al., 2020). This phenomenon could weaken the Allee effect
575 responsible for failure of a large number of biological invasions due to reduced individual
576 fitness in small populations (Yamaguchi, 2004; Mesgaran et al., 2016). Hybridization can also
577 help to increase fitness and invasive potential by improving biological traits such as fertility
578 (Schierenbeck & Ellstrand, 2009; Hovick & Whitney, 2014). For example, in the invasive ant
579 species *Solenopsis geminata* and *Solenopsis xyloni*, hybrids show a competitive advantage over

580 pure species, with hybrids being more aggressive than *S. xyloni* and foraging more efficiently
581 than *S. geminata* (Axen et al., 2014). In species within the *Tapinoma nigerrimum* complex,
582 hybrids, as in *Solenopsis*, can produce fertile offspring (Fournier & Aron, 2021). Therefore, we
583 might also expect to find competitive advantages in hybrids that would enhance their invasive
584 characteristics (Seifert et al., 2017; Fournier & Aron, 2021).

585 **4.3. Management implications**

586 Controlling the invasion routes and associated vectors remains the most appropriate
587 strategy for limiting biological invasions and mitigating their effects (Hulme, 2009; Pergl et al.,
588 2017). OPSOs make up the most visible part of the global plant trade, but large landscaping
589 operations such as new urban green spaces import plants through bulk importers or directly
590 from abroad. In addition, invasive ants can be introduced through various other means such as
591 soil transport, food product shipment, or even vehicular transportation (Suhr et al., 2019;
592 Siddiqui et al., 2021; Hsu et al., 2024). The establishment of these species in countries like the
593 Netherlands, a global leader in the production and export of ornamental plants, could result in
594 worrying large scale secondary spread and bridgehead effect (Van Tuyl, 2012; Javal et al., 2019;
595 Blumenfeld et al., 2021). Additionally, these species are thriving in anthropised habitats such
596 as urban areas (Centanni et al., 2022), which could potentially facilitate their invasion of other
597 similarly human-modified environments as suggested by Hufbauer et al., (2012)
598 («Anthropogenically Induced Adaptation to Invade», AIAI) and shown in the little fire ant,
599 *Wasmannia auropunctata* (Foucaud et al., 2013).

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

613 **Conclusion**

614 Overall, we reveal a pervasive and complex role of the ornamental plant trade (most
615 probably of trees requiring soil transport) in the human-mediated continental and regional
616 spread of three invasive ants of the *Tapinoma nigerrimum* complex in western Europe. Using
617 molecular markers, we linked *Tapinoma* ants found in OPSOs to regions supplying ornamental
618 plants, and most strikingly, showed that there are multiple source populations being
619 introduced into OPSOs. However, our results also highlight that the presence of invasive
620 species in OPSOs does not always translate into the invasion of the surrounding region. Indeed,
621 although we documented high propagule pressure of *Tapinoma magnum* in OPSOs in all
622 studied French regions, in Montpellier, where other species of the *Tapinoma nigerrimum*
623 complex occur natively, this invasive species was rare outside OPSOs. In contrast, outside the

624 Mediterranean regions, where no *Tapinoma* of the *nigerrimum* complex occur natively, invasive
625 *T. magnum* populations were found outside OPSOs. This research enhances our understanding
626 of a significant invasion pathway for ants and other invertebrates and stresses on the
627 importance of collaborating with OPSOs to prevent future introductions and limit ongoing
628 ones.

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Appendices

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(A) OPSOs

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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. ibercium</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

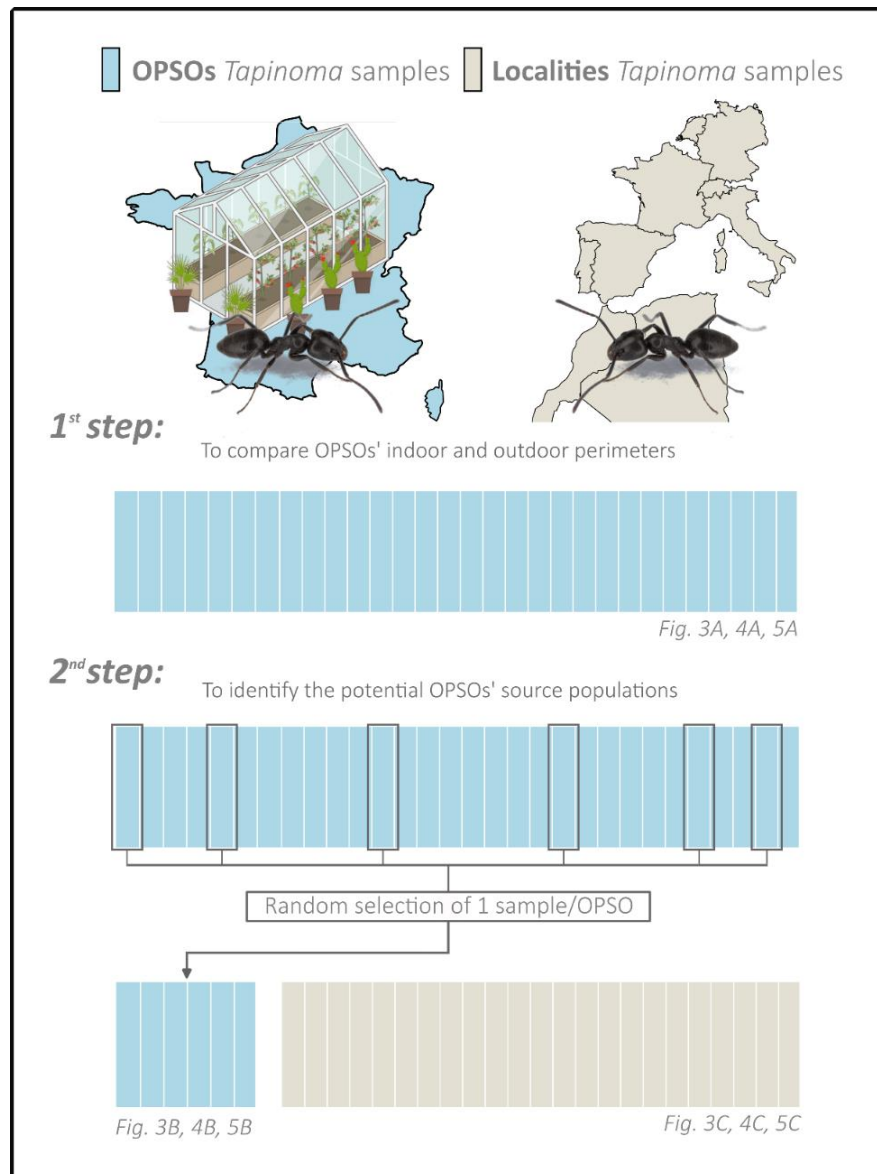
Species	Locality	Region	Potential species status	Sample date	Latitude	Longitude	n
<i>T. darioi</i>	Spain	Catalonia	Native	2014-2021	41.478186	1.606580	27
	M-France	Provence-Alpes-Côte d'Azur	Uncertain	2019-2023	43.358053	5.354571	13
	M-France	Occitanie	Probably native	2014-2023	43.664165	3.923175	119
	Italy	Lazio	Uncertain	2013-2014	41.886135,	12.392395	6
	Italy	Tuscany	Uncertain	2014	42.417	11.235	1
	Italy	Liguria	Uncertain	2014	44.149	9.685	1
	Corsica	Corsica	Exotic	2012-2016	41.37359	9.18058	4
	NM-France	Bourgogne -Franche-Comté	Exotic	2016	46.7749512	4.8580844	1
	NM-France	Hauts-de-France	Exotic	2019	49.20667	2.58578	1
	NM-France	Pays de la Loire	Exotic	2019-2022	47.248001	-2.259574	4
	NM-France	Nouvelle-Aquitaine	Exotic	2014	46.349727	-1.37036621	1
	Switzerland	Vaud	Exotic	2019	46.50557	6.65312	1
	<i>T. ibercium</i>	S-Portugal	Algarve	Native	2016	37.07544	-8.75598
N-Portugal		Norte	Native	2013	41.551083	-7.146007	2
S-Spain		Castilla-La Mancha	Native	2012-2019	38.915170	-3.833179	2
S-Spain		Region of Murcia	Native	2017	38.345	-1.493	1
S-Spain		Andalusia	Native	2012-2023	37.331403	-3.570793	13
N-Spain		Community of Madrid	Native	-	40.8672	-4.1003	3
N-Spain		Asturias	Native	2018	42.773069	-5.868145	1
M-France		Occitanie	Exotic	2019	43.42769	3.60826	1
M-France		Provence-Alpes-Côte	Exotic	2021-2023	43.644859	4.902519	2
Rotterdam		South Holland	Exotic	2017	51.9585	4.5077	1
Algeria		Bouria	Native	-	36.4468505	3.9460482	11
Algeria		Alger	Native	-	36.742	3.1199497	8
Morocco		Agmod	Native	2014	35.158	-4.326	2
Morocco	Tanger-Tetouan-Al Hoceima	Native	2023	35.0985533	-5.27418667	5	
Morocco	Fas-Meknas	Native	2023	33.91	-5.556	3	
Morocco	Sus-Massa	Native	2014	31.51212	-9.76765	4	
Sicily	Sicily	Native	2013-2018	37.387973	13.297286	35	
Aeolien is	Aeolien island	Native	2014	38.57794	14.81013	4	
Italy	Apulia	Native	2013	40.65	17.909	6	
Italy	Basilicata	Native	2013	40.837	16.036	2	
Italy	Campania	Native	2013	40.23079	14.9588	4	
Italy	Calabria	Native	2013	39.925	15.756	1	
Italy	Abruzzo	Native	2013	42.619	13.984	5	
Italy	Marche	Probably native	2013-2014	42.88398	13.33942	4	
Italy	Tuscany	Probably native	2017	43.765548	11.257823	1	
Italy	Liguria	Uncertain	2014	44.357	8.571	1	
Italy	Lazio	Probably native	2013-2014	41.711056	12.36278	20	
Sardinia	Sardinia	Exotic	2014	40.224633	9.625747	5	
Corsica	Corsica	Exotic	2009-2021	42.0038	8.9201	26	
M-France	Provence-Alpes-Côte d'Azur	Uncertain	2014-2023	43.12076	5.93977	31	
M-France	Occitanie	Probably exotic	2014-2021	43.446147	3.702157	16	
NM-France	Nouvelle-Aquitaine	Exotic	2008-2022	45.519045	-1.122327	6	
NM-France	Pays de la Loire	Exotic	2018-2022	47.285891	-2.512643	7	
NM-France	Bretagne	Exotic	2021	48.136565	-1.6939176	1	
NM-France	Normandie	Exotic	2022	49.100326	-1.0791	1	
NM-France	Auvergne-Rhone-Alpes	Exotic	2011-2023	45.741177	4.819881	15	
NM-France	Grand Est	Exotic	2019	48.661742	7.611926	2	
Switzerland	Vaud	Exotic	2017-2019	46.52156	6.64287	4	
Germany	Rhineland-Palatinate	Exotic	2009-2012	49.263	8.135	4	

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Appendix 1 – *Tapinoma* samples collected in (A) French OPSOs and (B) Western Europe and North Africa localities.



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Appendix 2 – 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 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 madeirense</i> ; <i>Temnothorax grp niger</i> ; <i>Temnothorax lichtensteini</i> ; <i>Temnothorax racovitzai</i> ; <i>Temnothorax recedens</i> ; <i>Temnothorax unifasciatus</i> ; <i>Tetramorium semilaeve</i>	<i>Aphaenogaster gibbosa</i> ; <i>Aphaenogaster senilis</i> ; <i>Camponotus aethiops</i> ; <i>Camponotus cruentatus</i> ; <i>Camponotus lateralis</i> ; <i>Cataglyphis piliscapa</i> ; <i>Crematogaster scutellaris</i> ; <i>Formica 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 recedens</i> ; <i>Temnothorax unifasciatus</i> ; <i>Tetramorium grp caespitum</i> ; <i>Tetramorium semilaeve</i> ; <i>Tetramorium sp. 1</i> ; <i>Plagiolepis schmitzii</i> ; <i>Lasius neglectus</i>

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Appendix 3 – Ant species of Montpellier OPSOs depending sampling perimeter

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696

Conflict of interest disclosure

697 The authors declare that they comply with the PCI rule of having no financial conflicts
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699

Data, scripts, code, and supplementary information availability

700 The Text uses the paragraph style "Text PCJ".

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

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