Title: Urbanisation and habitat fragmentation favour thermophilic and monogynous ant species

Authors: Basile Finand[1,2], Thibaud Monnin[1], Céline Bocquet[1], Angélique Bultelle[1], Pierre Fédérici[1], Léa Darmedru[1], Solène Gouffault[1], Joséphine Ledamoisel[1], Nicolas Loeuille[1]

[1]Sorbonne Université, Université Paris Cité, Université Paris Est Créteil, CNRS, INRAE, IRD, Institut d'Ecologie et des Sciences de l'Environnement de Paris (UMR7618), 75005 Paris, France

[2]Ecosystems and Environment Research Program, Faculty of Biological and Environmental Sciences, University of Helsinki, Helsinki, Finland

Corresponding author: Basile Finand, University of Helsinki Yliopistonkatu 3 00100 Helsinki Finland, finand.basile@gmail.com

Acknowledgements: We would like to thank the City of Paris and the Natural History Museum of Paris for allowing us to sample the parks of the city. We also thank Xavier Espadaler and Bernard Kaufmann for their help in the identification of some species.

Conflict of interest: The authors declare no conflict of interest.

Authorship statement: Basile Finand, Thibaud Monnin, and Nicolas Loeuille conceived the study. Basile Finand, Thibaud Monnin, Nicolas Loeuille, Léa Darmedru, Joséphine Ledamoisel, Céline Bocquet, Angélique Bultelle, Pierre Fédérici, and Solène Gouffault collected the data. Basile Finand analysed the data. Basile Finand, Thibaud Monnin, and Nicolas Loeuille wrote the paper. All the other co-authors agreed on the last version of the paper.

Data statement: Data and codes are available on Zenodo: https://zenodo.org/records/14792981

Abstract:

Environmental changes such as urbanisation and habitat fragmentation profoundly impact ecological communities by altering habitats, resources, and microclimate. Ants, with diverse life histories and strong ecological effects, are ideal models to study these pressures. We investigated the response of ant communities, including taxonomic and functional diversity, to urbanisation and habitat fragmentation in the Paris region, comparing 24 urban parks vs 25 rural forests outside the city. We found a clear difference in species composition between urban and rural environments, with a higher prevalence of monogynous and thermophilic species in the city. Forest communities are homogeneous across the three fragmentation levels we studied, while park communities differ noticeably depending on park size, with larger parks harbouring more species. Our findings suggest that urbanisation selects specific ant traits and favours more thermophilic species, thereby increasing the mean thermal preference of urban communities. These selective effects influence which species can colonise and survive in different patches, shaping metacommunity structure and potentially affecting the resilience of ant communities under climate change.

Keywords: Ants, heat island effect, metacommunity, trait selection, urbanisation

Introduction

Habitat fragmentation stands as a primary driver of biodiversity decline, exerting manifold impacts on ecosystems worldwide (Alberti, 2015; Aronson et al., 2014; Diamond & Martin, 2021; Haddad et al., 2015; Johnson & Munshi-South, 2017; Piano et al., 2020). This phenomenon is characterised by a reduction in total habitat size, with an increase in patch number, but smaller and more isolated (Fahrig, 2003). Habitat fragmentation impedes dispersal between populations, leading to direct impacts on individual and gene flows, resulting in population declines and reductions in genetic variability (Hastings, 1983; Travis et al., 2013; Young et al., 1996). These effects reverberate through ecological communities, altering their composition and dynamics. Habitat fragmentation gives rise to metacommunities, i.e. interconnected communities linked through dispersal. Metacommunity dynamics can happen in various ways depending on species and environmental characteristics (Leibold et al., 2004). In scenarios where variations in environmental conditions among patches do not play a key role, biodiversity hinges exclusively on the competitive abilities and colonisation capacities of species, a dynamic termed patch dynamic. Colonising species can exploit and establish populations in patches where competitors cannot persist (Tilman, 1994). Consequently, habitat fragmentation, through habitat destruction and isolation, is expected to favour colonising species while disadvantaging more competitive species, thereby reducing total diversity (Finand, Monnin, et al., 2024; Tilman et al., 1994). Conversely, in environments where variability among patches drives ecological dynamics, two dispersal-dependent mechanisms emerge. In scenarios with restricted dispersal, species diversity is governed by species sorting, where species whose ecological niches best match local conditions competitively exclude others within each patch. Conversely, when dispersal between patches is extensive, mass effects come into play (Mouquet & Loreau, 2003), allowing less-adapted species to persist in small numbers, being continually resupplied from surrounding patches, akin to source-sink dynamics. Although species sorting typically yields lower species richness per patch compared to mass effect, when dispersal is exceedingly high and mass effects dominate, all species compete for average metacommunity

conditions, leading to competitive exclusion at this scale. Diversity is then low, at the local and metacommunity scale (Mouquet & Loreau, 2003). The heightened fragmentation of habitat, by augmenting patch isolation, is expected to foster species sorting, consequently diminishing local species richness and increasing species turnover among patches. Finally, the neutral theory, akin to island biogeography (MacArthur & Wilson, 1967), posits that diversity is solely dependent on species loss through emigration and extinction balanced by gains through immigration and speciation, with no differentiation in species abilities (Hubbell, 2001). Importantly, these four paradigms can be disentangled based on variations in species composition and patterns of local (alpha), regional (gamma) diversity and variations in species composition among patches (beta diversity). For instance, if species sorting dominates, local composition should differ in contrasted environments so that beta diversity is mostly associated with a "turnover" component (sensu (Baselga, 2010)). Conversely, local dispersal in mass effects should lead to a spatial autocorrelation in species composition so that communities in harsher environments or smaller patches should be a subset of communities developing in better or larger patches. This enhances the "nestedness" component of beta diversity (sensu (Baselga, 2010)).

Urbanisation is another major factor affecting biodiversity. This transformative process reshapes environments in many ways, fostering novel ecological dynamics and posing significant challenges to native flora and fauna. First, urbanisation is most often associated with high habitat fragmentation (Haddad et al., 2015). Second, it also generates varied types of pollution, including chemicals, noise disturbance, and altered light regimes, often favouring species with specific adaptations or tolerances (Hölker et al., 2010; Newport et al., 2014). These pollutants permeate air, water, and soil, exerting deleterious effects on biotic components of ecosystems. Third, changes in resource availability represent another hallmark of urbanisation, including variations in quantity, quality, and seasonality (Hantak et al., 2021; Wilson & Jamieson, 2019). Finally, the creation of distinct microclimates within cities, characterised by elevated temperatures (urban heat island effect), exacerbates thermal stress on organisms and modifies ecosystem dynamics (Kaiser et al.,

88 2016; McGlynn et al., 2019). This thermal gradient can influence species distributions, phenology,
89 and physiological processes, driving community composition and structure shifts.

90 Beyond diversity indices, the specific environmental factors and the low connectivity
91 encountered in cities should select specific traits. Habitat fragmentation may favour low dispersal
92 (Cheptou et al., 2008; Finand et al., 2023), while higher temperatures promote species and
93 phenotypes whose thermal preference matches these conditions (Campbell-Staton et al., 2021;
94 Diamond et al., 2018). For instance, longer-legged species are selected in hotter parks in Taichung
95 City because the distance between the body and soil limits desiccation (Liu et al., 2019). In general,
96 urban and rural species may differ in many other traits (Buchholz & Egerer, 2020; Croci et al., 2008)
97 reflecting the multidimensional changes in such environments.

98 Insects and in particular ants have an important impact on ecosystems by dispersing seeds,
99 pollinating, participating in nutrient cycles, structuring the soil, and participating in food chains
100 (Hölldobler & Wilson, 1990). They are a very good model group to study the effects of urbanisation
101 and habitat fragmentation on communities. First, their life history traits are variable between
102 species. Some of these traits are strongly related to their dispersal abilities (size of individuals,
103 presence or absence of wings in queens) and competitiveness (size of colonies, diet), and therefore
104 play a key role as functional traits in metacommunity dynamics. Second, ants are abundantly present
105 and diverse in and outside cities, which allows direct comparative studies. Most ant species depend
106 on green spaces, which makes the city a very fragmented habitat compared to the countryside, even
107 if some species can live in built areas. Last, they are easy to sample. Several empirical studies have
108 shown that urbanisation and habitat fragmentation affect the species richness of ants, with a
109 decrease in species richness as urbanisation increases and a change in community composition
110 (Carpintero & Reyes-López, 2014; Ješovnik & Bujan, 2021; Leal et al., 2012; Pacheco & Vasconcelos,
111 2007; Theunis et al., 2005). For instance, climate and resource specialist ants are more sensitive to
112 habitat fragmentation (Leal et al., 2012). Moreover, this change in community composition due to

habitat fragmentation impacts ecosystem services provided by ants influencing decomposition and soil structure (Sanford et al., 2009).

Paris and its region offer a good opportunity to study urbanisation and habitat fragmentation, with a marked gradient from the very densely populated city centre to low-density areas thirty kilometres away. The city has numerous urban parks of various sizes, surrounded by a matrix of streets and buildings unsuitable for most ant species. This makes Parisian parks a perfect setup to understand the impact of fragmentation on ant communities. Moreover, the urban heat island effect within Paris is well-documented (Lemonsu et al., 2015). The surrounding region is more rural with many natural forests of various sizes allowing an interesting comparison with the city.

We here investigate the impact of urbanisation and habitat fragmentation on ant communities at different scales by comparing forest (low urbanisation and low fragmentation) and urban communities (high urbanisation and high fragmentation). We measured community differences between the two habitats, and the effects of the two main components of fragmentation, isolation, and patch size, within each habitat. We hypothesise that fragmentation decreases species richness and changes community structure, with more turnover than nestedness due to higher species sorting and lower mass effects. Furthermore, we studied variations in traits linked to thermal preference, colony social structure (queen number) and dispersal abilities. We hypothesise that the city harbours species that are more thermal-resistant due to the urban heat island effect, and that have short dispersal distances because of the high habitat fragmentation.

Material and methods

Patch selection

To study the impact of urbanisation and particularly of habitat fragmentation on litter ants, we sampled two different habitats: 25 rural forests in the Paris region and 24 wooded parts of urban parks within the city (Figure 1). Forests are considered minimally fragmented environments, as they offer a favourable habitat for litter ants and are surrounded by a matrix of habitats that, while less favourable, can still support ant species, e.g. hedges around agricultural fields or private gardens. On the contrary, parks are islands of favourable habitats (woods and shrubs) surrounded by a mostly hostile matrix (streets and buildings), though local refugia may exist. To compare the same litter ant communities in forests and parks, we targeted park areas with natural litter for sampling, i.e., areas under trees or shrubs. This allowed us to focus on the specific community of ants living in the litter and to make habitats as comparable as possible. Evidence that we sampled the forest litter ant community in parks is that the two species most abundant in our park samples are *Temnothorax nylanderi* and *Myrmecina graminicola*, which are particularly abundant in forests (Blatrix et al., 2013; Seifert, 2018) and also the most abundant ants in our forest samples (see results). Forests adjacent to the city are used here as reference communities to assess the effect of urbanisation, which intrinsically involves habitat change, as it is the closest environment to litter. Differences between park and forest habitats reflect spatial variations in niche conditions, which is precisely what this study aims to examine. We study the effect of urbanisation at the regional scale (city parks vs forests) and the effect of habitat fragmentation at the local scale (parks of various sizes and isolation, forests of various sizes).

We selected forest patches (n = 24) of three fragmentation classes (Figure 1a). Minimally fragmented forests (n = 10) had between 75 and 95% of forest cover within 1 Km, medium fragmented forests (n = 8) had between 30 and 70% of forest cover, and highly fragmented forests (n = 6) had less than 5% of forest cover in their surroundings. We used the database BD Forêt®

157 Version 2.0 from the "National Institute of Geographic and Forest Information" of France (IGN,
158 https://inventaire-forestier.ign.fr/carto/afficherCarto/V2, last visit: 19/07/2022) to assess forest
159 cover. Forest classes are evenly distributed around Paris, and we chose well-separated locations that
160 likely represent independent plots (mean distance = 52.1 +/- 23.7 Km, min = 6.4 Km, max = 122.1
161 Km).

162 Parks fragmentation was measured using two metrics, size and isolation. We selected parks
163 (n = 25) of three size classes (Figure 1b), namely large (n = 8, 80 000-250 000 m^2), medium (n = 9, 5
164 000-12 000 m^2), and small parks (n = 8, 500-2 000 m^2), and measured their isolation as the quantity
165 of green area (other parks) within 1 Km around the focal park boundaries. As for forests, we selected
166 parks that were evenly distributed within Paris and well separated, assumed to represent
167 independent points (mean distance = 4.9 +/- 2.1 Km, min = 552 m, max = 9.5 Km).

168 *Sampling*

169 We sampled forests between May and July 2020, between 11 am and 4 pm, on rainless days.
170 We distributed 12 quadrats of one square meter each, equally spaced every 9 m, along a transect of
171 100 m. We independently collected the litter and superficial soil on each of the 12 quadrats. We
172 collected organisms using the Winkler extraction method (Agosti et al., 2000). We detail the
173 procedure below.

174 We sampled parks between May and August 2021, between 11 am and 4 pm, on rainless
175 days. To compare the same litter ant communities in forests and parks, we targeted park areas with
176 natural litter for sampling, i.e. areas under trees or shrubs. It allows us to focus on the specific
177 community of ants living in the litter and make the habitats as comparable as possible with forests.
178 We purposefully placed the 12 quadrats into these areas and dispersed the quadrats within parks as
179 much as possible (considering the configuration of the parks, transect was not possible). One park
180 (OLB) was so small that only five quadrats could be placed and sampled, and owing to a disturbance
181 only ten quadrats were sampled in another park (MAS). The sampling and extraction protocols were

182 the same for parks and forests.

183 For each quadrat, we sifted the litter and the first centimetres of soil using a 1 cm^2 sieve
184 (Figure S1a). This removed leaves, twigs and stones and retained the soil and organisms within,
185 including ants. We kept what passed the sieve in large plastic bags until we returned to the
186 laboratory. There, we moved the litter to sieve bags that were hung in a Winkler extractor for 48
187 hours (Agosti et al., 2000) (Figure S1b). As the litter gradually dried out, organisms moved away and
188 fell into an alcohol-filled collecting vial. This method samples all the macrofauna living in the
189 collected soil and litter, including ant foragers present in the litter and parts of the colonies that nest
190 in the litter or superficially in the soil.

191 We sampled litter ants in forests and parks in two separate years (2020 and 2021) due to
192 logistical constraints and movement restrictions related to the COVID-19 pandemic. Note that ant
193 queens and colonies live several years, and that the sampling was done during the same season.
194 While fluctuations of abundances from one year to another are certainly possible, our analyses focus
195 on species presence/absence in each quadrat rather than abundance. We further discuss the
196 implications of our sampling scheme in the discussion section.

197 *Identification of ant species*

198 We identified ants at the species level using a binocular microscope and three identification
199 keys (Blatrix et al., 2013; Seifert, 2018); Galkowski & Lebas "Identification des *Myrmica*",
200 unpublished). In addition, *Temnothorax* and *Hypoponera* species were identified by Xavier
201 Espadaler, while *Tetramorium* species were identified by Bernard Kaufmann.

202 *Ant species traits*

203 We selected different species-level traits to test for the effect of urbanisation. Queen size,
204 worker size and colony size (number of individuals) were obtained from the bibliography for all
205 collected species (Blatrix et al., 2013; Seifert, 2018). In addition, colony mass was estimated as

206 worker size^3 X colony size. Because colony mass is directly linked to metabolic requirements (Brown
207 et al., 2004), we expect that it could vary between urban and forest sites, either due to changes in
208 resources or temperature regimes.

209 We also analysed the social structure of a colony, with two levels: monogyny (species with
210 typically one queen per colony) and polygyny (species with typically several queens per colony). This
211 trait is to some extent linked to dispersal as monogynous species often perform independent colony
212 foundation (long dispersal distance strategy but low competitivity) whereas polygynous species do
213 colony fission (short dispersal distance strategy but high competitivity) (Cronin et al., 2013; Keller,
214 1991).

215 Finally, for each species, we estimated thermophily based on a meridional index from
216 Daufresne et al. (2004) (Daufresne et al., 2004). Recent advances in ant thermal ecology have
217 highlighted more precise traits such as critical thermal limits, activity temperatures, or behavioural
218 tolerances (Nascimento et al., 2022; Parr & Bishop, 2022; Roeder et al., 2021). They are well-suited
219 to characterise precisely the thermal performances of a few species in a given environment.
220 However, they require live workers in significant numbers (20 to 30 workers per colony, more for
221 polymorphic species, and several colonies per species), making them incompatible with our sampling
222 protocol with Winklers. The meridional index is better suited for analysing diverse assemblages
223 across broad spatial scales, like in our study. In addition, it integrates factors other than thermal
224 resistance per se that may relate to thermal preference, e.g. circadian rhythm of activity, and it is
225 generalisable across taxa and compatible with studies on biogeographical shifts under climate
226 change. It provides a useful, scalable metric for detecting broad patterns of community shifts along
227 environmental gradients. Species were considered meridional if most of their distribution lies south
228 of Paris, with meridionality being calculated by (Paris latitude – minimum observed latitude) /
229 (maximum observed latitude – minimum observed latitude). The meridional index for a given species
230 is, therefore, close to one when Paris is at the northern limit of its distribution, and close to zero

231 when Paris is at the southern limit of its distribution. Minimum and maximum latitudes were
232 obtained for each species distribution from the antmap.org website (last visit: 28/02/2024; (Guénard
233 et al., 2017; Janicki et al., 2016)). Only the records considered to pertain to the native distribution
234 were considered. Following previous works, we use this index as a proxy of the thermal preference
235 of a species. A Parisian species at the northern limit of its distribution is more thermophilic than one
236 at the southern limit. Paris is farther north than the northern range limit for two species. We have
237 attributed 1, the highest value, to them.

238 To understand which traits are linked to urbanisation, we assign a value of urbanisation
239 preference for each species, calculated as the number of urban patches where the species has been
240 found divided by the total number of patches (urban and forest patches) where it has been found.
241 Strictly urban and forest species have urbanisation indices of one and zero, respectively.

242 *Analyses*

243 Statistical analyses were done with R v3.6.2 (R Core Team 2016). We checked that our
244 sampling was sufficient to sample the litter ant biodiversity with rarefaction curves and chao analysis
245 using the vegan package.

246 We studied alpha diversity as a function of urbanisation at the regional scale (forests vs.
247 parks) using ANOVAs. At the local scale (among parks and among forests), the observed species
248 richness and the Shannon index were analysed as a function of park size and isolation, and forest
249 fragmentation using ANOVAs. We checked that the data complied with application conditions using
250 the DHARMa package (Hartig, 2022), and log-transformed them when normality or homoscedasticity
251 were not satisfied.

252 We analysed beta diversity with Jaccard's dissimilarity index because we here focus on
253 species presence/absence rather than on abundance. Direct use of individual densities could be
254 problematic, as our sampling procedure can recover isolated individuals as well as whole colonies for

some *Temnothorax* species and *Myrmecina graminicola*. The second instance would inflate recorded abundances of superficial species compared to species nesting deeper in the soil for which we only collect foragers. We performed db-RDA (distance-based redundancy analysis), an RDA on dissimilarity distances, to assess if our environmental factors affect dissimilarity between our communities (Legendre & Anderson, 1999). We used ANOVAs to test the significance using the vegan package. We used the package *betapart* to assess the percentage of turnover and nestedness composing the dissimilarities between our communities (Baselga & Orme, 2012).

To link the urbanisation preference to species traits, we first checked the correlation among traits using a Pearson test. The different size measurements were highly correlated (Figure S2). We kept the total mass of a colony, as it contains the size of a colony and the weight of individuals. In the end, variations in three traits were explored: the total mass of a colony, the social structure, and the meridional index. To assess if the urbanisation preference of species is correlated with each trait, we performed a linear model for the colony mass and the meridional index and a generalised linear model with a binomial link function for the social structure. We tested the application conditions (normality, homoscedasticity) using the DHARMa package (Hartig, 2022). We log-transformed the total mass.

Results

We collected and identified 36 361 ants from 12 genera and 29 species. Abundances are similar in forests and parks (18 094 and 18 267 ants, respectively). Similarly, the number of species recovered per habitat type is comparable (Figure 2, 23 species in forests and 20 species in parks). 14 species occurred in both parks and forests, albeit in most cases with different relative abundances, while 9 species occurred in forests and 6 in parks only (Figure 2). One invasive species only was recorded (*Lasius neglectus*). Removing it from the analyses does not qualitatively change the results.

Sampling effort

The rarefaction curves and the chao analyses show that the sampling was sufficient to estimate litter ant diversity (Figure S3). Indeed, we sampled 95.19 +/- 25.41 % of the theoretical number of species in forests and 91.13 +/- 13.12 % in parks. Only two forests (CSM and GIF) and three parks (HEA, HEG and PDG) have a percentage of observed species representing less than 80% of the theoretical number of species. However, this theoretical number of species is higher in these patches (around or above 15) than in the other patches (usually around 10, seldom higher than 12) so it may be overestimated. Therefore, we use the observed number of species per patch in the analyses.

Urbanisation effect at the regional scale (forests vs parks)

Unexpectedly, we found more species locally with increased urbanisation (F value = 6.67, p = 0.013, R^2 = 10.6%, Figure 3a). Indeed, parks support 8.96 +/- 1.74 species while forest sites have 7.58 +/- 2.30 species. In agreement with this, the Shannon index is higher in the city environment showing a higher diversity with less dominant species (T value = 2.808, p = 0.007, R^2 = 13%, Figure 3d).

Urbanisation also influences species composition (F value = 28.47, p = 0.001, R^2 = 37.7%, Figure 4a). Communities are clearly different between parks and forests, with 89% of the beta diversity due to turnover (Jaccard index = 0.517, Figure 2), suggesting a dominant role of species sorting.

Fragmentation effect at the local scale

The fragmentation level at the local scale has no effect. In forests, it does not affect species richness (F value = 0.17, p = 0.84, Figure 3c), Shannon index (F value = 0.488, p = 0.62, Figure 3f) or the composition of ant communities (F value = 1.37, p = 0.128, Figure 4c). Similarly, for parks, isolation does not affect species richness (t value = -1.677, p = 0.107, Figure S4a), Shannon index (t

303 value = -1.866, p = 0.075, Figure S4b) or ant communities composition (F = 0.77, p = 0.69).

304 *Effect of park size*

305 As expected, larger parks harbour more species than smaller parks (F = 3.74, p = 0.039, R^2 =
306 0.19, Figure 3b). The effect is significant between small and large parks (pairwise comparison: large-
307 medium p = 0.21, medium-small p = 0.57, large-small p = 0.03). Large parks have on average 8 +/- 2.7
308 species, medium parks have 7.38 +/- 2.07 species and small ones have 7.17 +/- 2.14 species. Patch
309 size has a similar but marginal influence on the Shannon index (F value = 2.83, p = 0.081, Figure 3e).

310 Patch size also affects the spatial turnover of ant communities (F value = 2.14, p = 0.008, R^2 =
311 16.3%, Figure 4b). The beta diversity is composed of 100% of turnover between large and medium
312 parks, 84% between medium and small, and 93% between large and small (Jaccard index large-
313 medium = 0.222; medium-small = 0.278; large-small = 0.450) highlighting a dominant role of species
314 sorting.

315 *Effect of urbanisation on species traits*

316 There is no effect of urbanisation on the total mass of a colony (t value = -0.76, p = 0.46,
317 Figure 5a). However, it is correlated with the social structure (z value = -2.26, p = 0.02, R2 = 0.15,
318 Figure 5b), with more monogynous species in urban habitats. It is also correlated with a higher
319 meridional index, meaning that urban environments tend to select thermophilic ant species (t value
320 = 2.89, p = 0.008, R2 = 0.21, Figure 5c).

321

322 **Discussion**

323 Our study shows that urbanisation and the associated habitat fragmentation influence the
324 litter ant communities at the metacommunity scale. Surprisingly, the ant biodiversity assessed by
325 the total number of species per environment (gamma diversity) is stable, and the species richness
326 per patch is slightly higher in parks than in forests. Communities differ markedly between the two

environments, with a strong turnover in species compositions. At a local scale (alpha diversity), species richness and community composition are affected by park size and do not vary among forests. Finally, we highlight that the turnover in species composition between urban and forest patches is associated with systematic differences in species phenotypes. Urbanisation selects species that tend to be monogynous and thermophilic.

A possible limitation of our study is that forests and urban parks were sampled in different years (2020 vs. 2021). While we acknowledge this issue, we however think that potential biases are here limited. A first reason stems from the fact that our method relies on community composition (presence/absence of species), not on species abundances. While abundances may fluctuate from a year to another, we do not expect such variations when looking at the presence/absence of long-lived species. Ant queens and colonies are indeed long-lived (Hölldobler & Wilson, 1990). Ant queens live on average 10 years, up to 28 years, and colonies outlive queens in species where colonies have several queens or where queens can be replaced, e.g. by adoption of daughter queens (Keller, 1998). The composition of ant species community is therefore relatively stable from one year to the other (Donoso, 2017; Herbers, 2011). Focusing on species presence/absence, therefore reduces sensitivity to yearly fluctuations in colony size or activity. The clear differences observed between forests and parks align with ecological gradients (urbanisation, fragmentation, microclimate) rather than temporal effects. Notably, 2020 (forest sampling) was warmer in the Paris region than 2021 (park sampling, 2020: 14.3 °C, 2021: 12.9 °C. Source: opendata.paris.fr), yet we still detected thermophilisation in parks, which strengthens our inference. Finally, both habitats were sampled in the same season during no rain days, with sufficient effort to capture nearly all expected species (Fig. S3). Taken together, these points support that the observed differences reflect genuine ecological responses to urbanisation and fragmentation rather than temporal sampling artefacts.

At a regional scale, comparing rural versus urban environments reveals no differences in the total number of species but a clear difference in community composition, with beta diversity

352 dominated by its turnover component. This suggests that dispersal is low between the two
353 environments, creating different communities adapted to each, and highlights species sorting as a
354 strong regional-scale mechanism in this metacommunity. Indeed, if dispersal between forest and
355 urban sites was high, we would expect either community composition to be similar (low beta
356 diversity) or, if colonisation success differed between the environments, that the communities of
357 one environment would be a subset of the communities of the other environment (high nestedness,
358 (Baselga, 2010)). Differences in community composition between forests and parks can also reflect
359 differences in fragmentation and shifts in ecological niches. In parks, wooded areas represent only a
360 portion of the park and are often non-contiguous and surrounded by open habitats, allowing
361 workers from these patches to forage in the sampled litter. In contrast, even the most fragmented
362 forest patches were large enough to allow sampling away from the forest edge. Climate represents
363 another niche axis: parks are warmer due to the urban heat island effect, attracting warm-adapted
364 species, as confirmed by our results. Urbanisation also introduces various pollutants, which may
365 select for particular species and traits. These niche changes, inherent to urban environments, likely
366 contribute to the observed differences in community composition.

367 Surprisingly, more species are present per urban park than per forest. Several explanations
368 can be proposed. First, as mentioned above, species sorting dominates, suggesting restricted
369 dispersal between forests and city parks, and parks may thus host more ant species than forests if
370 they harbour a higher diversity of habitats and microenvironments. Although our sampling within
371 parks targeted shaded litter patches under bushes or trees to mimic forest conditions, they were
372 often surrounded by more open and trampled areas, potentially creating a range of microhabitats.
373 This aspect, not fully quantifiable in our study due to a lack of direct microhabitat characterisation,
374 could contribute to higher species richness in parks. However, if parks were richer simply because of
375 a higher microhabitat heterogeneity, we would expect to find a high nestedness. Instead, our data
376 reveal a near-complete turnover in species composition between forests and parks, suggesting that
377 parks do not merely add species but rather replace forest species with species better adapted to

urban conditions. Since warmer climates support more species, parks may receive a larger pool of colonisers, potentially increasing their species richness. This is confirmed with the trait analysis, where we have more warm-adapted species in the parks. Another possibility is that species richness in parks might be "inflated" by continuous colonisation processes such as soil inputs during park maintenance or transport of material within urban areas. These hypotheses would implicitly question our view of forests being good patches compared to parks. An alternative explanation would be that forests are (or have been until relatively recently) well-connected and form a metacommunity of their own. If so, high dispersal among forests could homogenise ant forest communities through mass effects, leading to a depressed lower alpha diversity reflecting partial homogenization (Leibold et al., 2004; Mouquet & Loreau, 2003). In contrast, when dispersal is low, as may be the case between parks, competition occurs independently within each park resulting in different communities hence higher alpha and gamma diversities. This increases turnover between patches as observed in our data. This is likely given that parks were made for human leisure and differ more from one another than natural forests do.

Our observations of local community compositions support the idea of strong mass effects among forests. Indeed, there is no difference in species richness and species composition among forests, even for the most fragmented ones. This suggests a high degree of dispersal between forest sites, which homogenises the communities. This is plausible because the matrix separating forests is less hostile than the one separating parks. Indeed, field hedges, roadsides and private gardens may connect forests by a network of trees and shrubs producing leaf litter and facilitating the dispersal of ants. Moreover, forests may be more similar to one another than parks. The former evolved from natural forests and have been managed largely for similar usages (e.g. wood production, leisure, hunting), whereas the latter are artificial and have to some extent been conceived to differ from one another to provide varied scenic environments. This could be confirmed by a more systematic study of biotic and abiotic environmental variations. If so, such homogeneity could limit the number of local niches, hence species sorting.

404 In urban areas, on a park scale, species richness is generally lower in smaller parks, and
405 community composition differs due to high species turnover. This pattern aligns with the classical
406 species-area relationship, which links larger areas to higher diversity (Preston, 1962), potentially
407 reflecting intensified species sorting in smaller parks (Leibold et al., 2004; Mouquet & Loreau, 2003).
408 In smaller parks, competitive exclusion may be more pronounced, as only the most competitive
409 species persist, while low dispersal limits the arrival of new species. This limited dispersal is
410 exacerbated by the hostile urban matrix surrounding these parks, which restricts movement and
411 colonisation, particularly in smaller parks less accessible through natural or human-mediated
412 dispersal (e.g., fewer plants or materials introduced). Consequently, these combined niche and
413 dispersal effects contribute to lower alpha diversity and higher turnover between smaller parks.
414 These patterns are consistent with other studies, including other ant communities. Smaller parks in
415 highly urbanized zones tend to harbour fewer ant species than those in peri-urban, less isolated
416 areas (Pacheco & Vasconcelos, 2007), while within cities, larger parks generally support greater
417 alpha diversity (Carpintero & Reyes-López, 2014). This trend extends to other ecosystems and taxa.
418 For example, forests show similar patterns (Leal et al., 2012). Other studies on isolated zooplankton
419 communities in controlled environments also report reduced diversity due to limited dispersal
420 (Steiner & Asgari, 2022), mirroring the low mass effects in our urban ant metacommunity. Such
421 findings are consistent with island biogeography theory, which suggests that isolated habitats, like
422 urban parks or fragmented forests, host fewer species than more contiguous areas (Ramalho et al.,
423 2022).

424 Beyond the turnover in species composition, we highlight that phenotypic traits are
425 deterministically associated with community variations. Urban species are more often monogynous
426 and more thermophilic. While the second trait was expected, given the heat island effect in cities,
427 the first was not. Monogyny is somewhat linked to dispersal capacity (Keller, 1991; Sundström et al.,
428 2005). Monogynous colonies are often founded by winged queens that disperse alone by flying over
429 long distances. In contrast, polygynous colonies are either founded by related non-flying queens that

430 disperse on foot over short distances with workers or arise secondarily by non-flying queens that
431 remain in their natal colony. Theoretically, habitat fragmentation can select for high dispersal (i.e.
432 winged queens), for instance, when dispersal is traded off with competition capacity (Finand,
433 Monnin, et al., 2024; Tilman, 1994), when fragmentation leads to high kin competition in remaining
434 patches, or to avoid inbreeding (Cote et al., 2017; Gandon, 1999; Hamilton & May, 1977). Some
435 empirical studies support these theoretical results, including in ants. For instance, at the intraspecific
436 level, colonisation ability can be in a trade-off with competition in an ant species (Finand, Loeuille, et
437 al., 2024). This selection for high dispersal in a fragmented context could explain, as a byproduct,
438 that city parks harbour more monogynous species because polygynous species disperse less.
439 However, some studies have shown opposite results, with habitat fragmentation in cities selecting
440 for lower dispersal (Cheptou et al., 2008; Finand et al., 2023). Indeed, while habitat fragmentation
441 usually favours high dispersal, it may have the opposite effect under some circumstances (e.g. highly
442 hostile matrix increasing dispersal costs, Bonte et al. 2012; Hastings 1983). A second explanation is
443 that monogynous species can be considered as pursuing spatial bet-hedging because flying queens
444 can access and distribute the risks on more patches than walking queens. Indeed, a colony producing
445 flying queens can attempt to establish new colonies on many patches. In contrast, a colony
446 producing apterous queens produces a few only, as each requires the allocation of workers, and
447 they have restricted dispersal, hence it has few establishment attempts. A bet-hedging strategy is
448 selected under temporally variable environments (Slatkin, 1974). City patches may be more variable,
449 due to many disturbances associated with human activities, and parks surrounded by unfavourable
450 environments. Having winged queens will increase the probability of having offspring in a more
451 favourable environment. A third hypothesis is that urban parks are relatively new, particularly
452 regarding ants that have a longer generation time than most other insects. The first species
453 colonising a new patch are the most dispersive ones, which in ants have winged queens and thus are
454 monogynous. Dispersal limitation also likely lasts in this highly fragmented context. Forests being
455 much older, the less dispersive but more competitive species had the time to colonise them and

456 progressively exclude better colonisers. All these hypotheses are not exclusive. Other taxa have
457 shown this shift in community composition with more dispersive species in the city, like carabid
458 beetles (Piano et al., 2017).

459 The high abundance of thermophilic ants in urban areas aligns with numerous studies
460 indicating that cities, such as Paris, are subject to the Urban Heat Island effect (Lemonsu et al.,
461 2015). Heat-susceptible species may disappear, and thermophilic species may dominate
462 communities in cities. Parr and Bishop (2022) suggest that temperate ant species may be less
463 vulnerable to climate warming than tropical species, and in some cases might even benefit from
464 rising temperatures. However, our findings—showing a near-complete replacement of forest ant
465 communities by species with more southern affinities in urban parks—do not fully support this idea.
466 On the contrary, although temperature is not the only factor differing between urban and rural
467 forests, our results suggest that our temperate ant communities living in forests may be negatively
468 impacted by rising temperatures. The prevalence of thermophilic species in urban areas has been
469 documented not only in ants but also in other groups, such as carabid beetles (Piano et al., 2017)
470 and moths (Franzén et al., 2020). More broadly, the process of thermophilisation, where
471 communities shift toward species that prefer warmer conditions due to rising temperatures, has also
472 been observed in non-urban ecosystems, including fish (Daufresne et al., 2004) and plants (Feeley et
473 al., 2020). This result is particularly relevant in the context of climate change, as temperatures are
474 expected to rise in the coming decades, leading to significant ecological consequences (McCarty,
475 2001). Cities offer a valuable natural laboratory for studying the impacts of climate change, with
476 urban communities serving as ideal experimental units to investigate these effects. Furthermore, our
477 findings suggest that climate change could act as a critical filter for community composition,
478 potentially leading to the decline of less thermophilic species. While urban areas might serve as
479 reservoirs for future biodiversity under changing climates, they will likely become increasingly
480 inhospitable for many species as climate change progresses.

References

Agosti, D., Majer, J. D., Alonso, L. E., & Schultz, T. R. (2000). *Ants: standard methods for measuring and monitoring biodiversity* (Smithsonia).

Alberti, M. (2015). Eco-evolutionary dynamics in an urbanizing planet. *Trends in Ecology & Evolution*, *30*(2), 114–126. https://doi.org/10.1016/j.tree.2014.11.007

Aronson, M. F. J., La Sorte, F. A., Nilon, C. H., Katti, M., Goddard, M. A., Lepczyk, C. A., Warren, P. S., Williams, N. S. G., Cilliers, S., Clarkson, B., Dobbs, C., Dolan, R., Hedblom, M., Klotz, S., Kooijmans, J. L., Kühn, I., MacGregor-Fors, I., McDonnell, M., Mörtberg, U., … Winter, M. (2014). A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1780), 20133330. https://doi.org/10.1098/rspb.2013.3330

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, *19*(1), 134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x

Baselga, A., & Orme, C. D. L. (2012). betapart: an R package for the study of beta diversity. *Methods in Ecology and Evolution*, *3*(5), 808–812. https://doi.org/10.1111/j.2041-210X.2012.00224.x

Blatrix, R., Galkowski, C., Lebas, C., & Wegnez, P. (2013). *Fourmis de France* (Delachaux).

Bonte, D., Dyck, H. Van, Bullock, J. M., Delgado, M., Gibbs, M., Lehouck, V., Matthysen, E., Mustin, K., Schtickzelle, N., Stevens, V. M., Vandewoestijne, S., Baguette, M., Barton, K., Benton, T. G., Chaput-bardy, A., Dytham, C., Hovestadt, T., Meier, C. M., Steve, C. F., … Travis, J. M. J. (2012). Costs of dispersal. *Biological Reviews*, *87*, 290–312. https://doi.org/10.1111/j.1469-185X.2011.00201.x

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, *85*(7), 1771–1789. https://doi.org/10.1890/03-9000

Buchholz, S., & Egerer, M. H. (2020). Functional ecology of wild bees in cities: towards a better understanding of trait-urbanization relationships. *Biodiversity and Conservation*, *29*(9–10), 2779–2801. https://doi.org/10.1007/s10531-020-02003-8

Campbell-Staton, S. C., Velotta, J. P., & Winchell, K. M. (2021). Selection on adaptive and maladaptive gene expression plasticity during thermal adaptation to urban heat islands. *Nature Communications*, *12*(1), 6195. https://doi.org/10.1038/s41467-021-26334-4

Carpintero, S., & Reyes-López, J. (2014). Effect of park age, size, shape and isolation on ant assemblages in two cities of Southern Spain. *Entomological Science*, *17*, 41–51. https://doi.org/10.1111/ens.12027

Cheptou, P.-O., Carrue, O., Rouifed, S., & Cantarel, A. (2008). Rapid evolution of seed dispersal in an urban environment in the weed *Crepis sancta*. *Proceedings of the National Academy of Sciences*, *105*(10), 3796–3799. https://doi.org/10.1073/pnas.0708446105

Cote, J., Bestion, E., Jacob, S., Travis, J., Legrand, D., & Baguette, M. (2017). Evolution of dispersal strategies and dispersal syndromes in fragmented landscapes. *Ecography*, *40*, 56–73. https://doi.org/10.1111/ecog.02538

Croci, S., Butet, A., & Clergeau, P. (2008). Does urbanization filter birds on the basis of their biological traits? *The Condor*, *110*(2), 223–240. https://doi.org/10.1525/cond.2008.8409

Cronin, A. L., Molet, M., Doums, C., Monnin, T., & Peeters, C. (2013). Recurrent Evolution of Dependent Colony Foundation Across Eusocial Insects. *Annual Review of Entomology*, *58*(1), 37–55. https://doi.org/10.1146/annurev-ento-120811-153643

Daufresne, M., Roger, M. C., Capra, H., & Lamouroux, N. (2004). Long-term changes within the invertebrate and fish communities of the Upper Rhône River: effects of climatic factors. *Global Change Biology*, *10*(1), 124–140. https://doi.org/10.1046/j.1529-8817.2003.00720.x

Diamond, S. E., Chick, L. D., Perez, A., Strickler, S. A., & Martin, R. A. (2018). Evolution of thermal tolerance and its fitness consequences: parallel and non-parallel responses to urban heat islands across three cities. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1882), 20180036. https://doi.org/10.1098/rspb.2018.0036

Diamond, S. E., & Martin, R. A. (2021). Evolution in Cities. *Annual Review of Ecology, Evolution, and Systematics*, *52*(1), 519–540. https://doi.org/10.1146/annurev-ecolsys-012021-021402

Donoso, D. A. (2017). Tropical ant communities are in long-term equilibrium. *Ecological Indicators*, *83*, 515–523. https://doi.org/10.1016/j.ecolind.2017.03.022

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, *34*, 487–515. https://doi.org/10.1146/annurev.ecolsys.34.011802.132419

Feeley, K. J., Bravo-Avila, C., Fadrique, B., Perez, T. M., & Zuleta, D. (2020). Climate-driven changes in the composition of New World plant communities. *Nature Climate Change*, *10*(10), 965–970. https://doi.org/10.1038/s41558-020-0873-2

Finand, B., Loeuille, N., Bocquet, C., Fédérici, P., Ledamoisel, J., & Monnin, T. (2023). Habitat fragmentation through urbanization selects for low dispersal in an ant species. *Oikos*. https://doi.org/10.1111/oik.10325

Finand, B., Loeuille, N., Bocquet, C., Fédérici, P., & Monnin, T. (2024). Solitary foundation or colony fission in ants: an intraspecific study shows that worker presence and number increase colony foundation success. *Oecologia*, *204*(3), 517–527. https://doi.org/10.1007/s00442-023-05509-4

Finand, B., Monnin, T., & Loeuille, N. (2024). Evolution of dispersal and the maintenance of fragmented metapopulations. *Oikos*, *2024*(2). https://doi.org/10.1111/oik.10490

Franzén, M., Betzholtz, P.-E., Pettersson, L. B., & Forsman, A. (2020). Urban moth communities suggest that life in the city favours thermophilic multi-dimensional generalists. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1928), 20193014. https://doi.org/10.1098/rspb.2019.3014

Gandon, S. (1999). Kin Competition, the Cost of Inbreeding and the Evolution of Dispersal. *Journal of Theoretical Biology*, *200*(4), 345–364. https://doi.org/10.1006/jtbi.1999.0994

Guénard, B., Weiser, M. D., Gómez, K., Narula, N., & Economo, E. P. (2017). The Global Ant Biodiversity Informatics (GABI) database: synthesizing data on the geographic distribution of ant species (Hymenoptera: Formicidae). *Myrmecological News*, *24*, 83–89. https://doi.org/https://doi.org/10.25849/myrmecol.news_024:083

Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., Lovejoy, T. E., Sexton, J. O., Austin, M. P., Collins, C. D., Cook, W. M., Damschen, E. I., Ewers, R. M., Foster, B. L., Jenkins, C. N., King, A. J., Laurance, W. F., Levey, D. J., Margules, C. R., … Townshend, J. R. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, *1*(2). https://doi.org/10.1126/sciadv.1500052

Hamilton, W. D., & May, R. M. (1977). Dispersal in stable habitats. *Nature*, *269*(5629), 578–581. https://doi.org/10.1038/269578a0

Hantak, M. M., McLean, B. S., Li, D., & Guralnick, R. P. (2021). Mammalian body size is determined by interactions between climate, urbanization, and ecological traits. *Communications Biology*, *4*(1), 972. https://doi.org/10.1038/s42003-021-02505-3

Hartig, F. (2022). *DHARMa: Residual diagnostics for hierarchical (multi-Level / mixed) regression models*. R package version 0.4.6. https://CRAN.R-project.org/package=DHARMa

Hastings, A. (1983). Can spatial variation alone lead to selection for dispersal? *Theoretical Population Biology*, *24*, 244–251. https://doi.org/10.1016/0040-5809(83)90027-8

Herbers, J. M. (2011). Nineteen years of field data on ant communities (Hymenoptera: Formicidae): What can we learn? *Myrmecological News*, *15*, 43–52. https://doi.org/https://doi.org/10.25849/myrmecol.news_015:043

Hölker, F., Wolter, C., Perkin, E. K., & Tockner, K. (2010). Light pollution as a biodiversity threat. *Trends in Ecology & Evolution*, *25*(12), 681–682. https://doi.org/10.1016/j.tree.2010.09.007

Hölldobler, B., & Wilson, E. O. (1990). *The ants* (Harvard University Press, Ed.).

Hubbell, S. P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press.

Janicki, J., Narula, N., Ziegler, M., Guénard, B., & Economo, E. P. (2016). Visualizing and interacting with large-volume biodiversity data using client–server web-mapping applications: The design and implementation of antmaps.org. *Ecological Informatics*, *32*, 185–193. https://doi.org/10.1016/j.ecoinf.2016.02.006

Ješovnik, A., & Bujan, J. (2021). Wooded areas promote species richness in urban parks. *Urban Ecosystems*, *24*(6), 1305–1315. https://doi.org/10.1007/s11252-021-01112-8

Johnson, M. T. J., & Munshi-South, J. (2017). Evolution of life in urban environments. *Science*, *358*(6363), eaam8327. https://doi.org/10.1126/science.aam8327

Kaiser, A., Merckx, T., & Van Dyck, H. (2016). The Urban Heat Island and its spatial scale dependent impact on survival and development in butterflies of different thermal sensitivity. *Ecology and Evolution*, *6*(12), 4129–4140. https://doi.org/10.1002/ece3.2166

Keller, L. (1991). Queen number, mode of colony founding, and queen reproductive success in ants (Hymenoptera Formicidae). *Ethology Ecology & Evolution*, *3*(4), 307–316. https://doi.org/10.1080/08927014.1991.9525359

Keller, L. (1998). Queen lifespan and colony characteristics in ants and termites. *Insectes Sociaux*, *45*(3), 235–246. https://doi.org/10.1007/s000400050084

Leal, I. R., Filgueiras, B. K. C., Gomes, J. P., Iannuzzi, L., & Andersen, A. N. (2012). Effects of habitat fragmentation on ant richness and functional composition in Brazilian Atlantic forest. *Biodiversity and Conservation*, *21*(7), 1687–1701. https://doi.org/10.1007/s10531-012-0271-9

Legendre, P., & Anderson, M. J. (1999). Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. *Ecological Monographs*, *69*(1), 1–24. https://doi.org/https://doi.org/10.1890/0012-9615(1999)069[0001:DBRATM]2.0.CO;2

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt, R. D., Shurin, J. B., Law, R., Tilman, D., Loreau, M., & Gonzalez, A. (2004). The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters*, *7*(7), 601–613. https://doi.org/10.1111/j.1461-0248.2004.00608.x

Lemonsu, A., Viguié, V., Daniel, M., & Masson, V. (2015). Vulnerability to heat waves: Impact of urban expansion scenarios on urban heat island and heat stress in Paris (France). *Urban Climate*, *14*, 586–605. https://doi.org/10.1016/j.uclim.2015.10.007

Liu, K.-L., Peng, M.-H., Hung, Y.-C., & Neoh, K.-B. (2019). Effects of park size, peri-urban forest spillover, and environmental filtering on diversity, structure, and morphology of ant assemblages in urban park. *Urban Ecosystems*, *22*(4), 643–656. https://doi.org/10.1007/s11252-019-00851-z

MacArthur, R. H., & Wilson, E. O. (1967). *The Theory of Island Biogeography*. Princeton University Press. https://doi.org/10.1515/9781400881376

McCarty, J. P. (2001). Ecological Consequences of Recent Climate Change. *Conservation Biology*, *15*(2), 320–331. https://doi.org/10.1046/j.1523-1739.2001.015002320.x

McGlynn, T. P., Meineke, E. K., Bahlai, C. A., Li, E., Hartop, E. A., Adams, B. J., & Brown, B. V. (2019). Temperature accounts for the biodiversity of a hyperdiverse group of insects in urban Los Angeles. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1912), 20191818. https://doi.org/10.1098/rspb.2019.1818

Mouquet, N., & Loreau, M. (2003). Community patterns in source-sink metacommunities. *The American Naturalist*, *162*(5), 544–557. https://doi.org/10.1086/378857

Nascimento, G., Câmara, T., & Arnan, X. (2022). Critical thermal limits in ants and their implications under climate change. *Biological Reviews*, *97*(4), 1287–1305. https://doi.org/10.1111/brv.12843

Newport, J., Shorthouse, D. J., & Manning, A. D. (2014). The effects of light and noise from urban development on biodiversity: Implications for protected areas in Australia. *Ecological Management & Restoration*, *15*(3), 204–214. https://doi.org/10.1111/emr.12120

Pacheco, R., & Vasconcelos, H. L. (2007). Invertebrate conservation in urban areas: Ants in the Brazilian Cerrado. *Landscape and Urban Planning*, *81*(3), 193–199. https://doi.org/10.1016/j.landurbplan.2006.11.004

Parr, C. L., & Bishop, T. R. (2022). The response of ants to climate change. *Global Change Biology*, *28*(10), 3188–3205. https://doi.org/10.1111/gcb.16140

Piano, E., De Wolf, K., Bona, F., Bonte, D., Bowler, D. E., Isaia, M., Lens, L., Merckx, T., Mertens, D., van Kerckvoorde, M., De Meester, L., & Hendrickx, F. (2017). Urbanization drives community

shifts towards thermophilic and dispersive species at local and landscape scales. *Global Change Biology*, *23*(7), 2554–2564. https://doi.org/10.1111/gcb.13606

Piano, E., Souffreau, C., Merckx, T., Baardsen, L. F., Backeljau, T., Bonte, D., Brans, K. I., Cours, M., Dahirel, M., Debortoli, N., Decaestecker, E., De Wolf, K., Engelen, J. M. T., Fontaneto, D., Gianuca, A. T., Govaert, L., Hanashiro, F. T. T., Higuti, J., Lens, L., … Hendrickx, F. (2020). Urbanization drives cross-taxon declines in abundance and diversity at multiple spatial scales. *Global Change Biology*, *26*(3), 1196–1211. https://doi.org/10.1111/gcb.14934

Preston, F. W. (1962). The Canonical Distribution of Commonness and Rarity: Part I. *Ecology*, *43*(2), 185. https://doi.org/10.2307/1931976

R Core Team. (2022). R: A language and environment for statistical computing. *R Foundation for Statistical Computing, Vienne, Au*. https://www.R-project.org/

Ramalho, W. P., With, K. A., de Sousa Mesquita, G., de Arruda, F. V., Guerra, V., Ferraz, D., Andrade, M. S., & do Prado, V. H. M. (2022). Habitat fragmentation rather than habitat amount or habitat split reduces the diversity and abundance of ground-dwelling anurans within forest remnants of the Brazilian Cerrado. *Journal for Nature Conservation*, *69*, 126259. https://doi.org/10.1016/j.jnc.2022.126259

Roeder, K. A., Roeder, D. V, & Bujan, J. (2021). Ant Thermal Tolerance: A Review of Methods, Hypotheses, and Sources of Variation. *Annals of the Entomological Society of America*, *114*(4), 459–469. https://doi.org/10.1093/aesa/saab018

Sanford, M. P., Manley, P. N., & Murphy, D. D. (2009). Effects of Urban Development on Ant Communities: Implications for Ecosystem Services and Management. *Conservation Biology*, *23*(1), 131–141. https://doi.org/10.1111/j.1523-1739.2008.01040.x

Seifert, B. (2018). *The Ants of Central and Northern Europe*. Lutra Verlags- und Vertriebsgesellschaft.

Slatkin, M. (1974). Hedging one's evolutionary bets. *Nature*, *250*(5469), 704–705. https://doi.org/10.1038/250704b0

Steiner, C. F., & Asgari, M. (2022). Habitat isolation reduces intra- and interspecific biodiversity and stability. *Royal Society Open Science*, *9*(2). https://doi.org/10.1098/rsos.211309

Sundström, L., Seppä, P., & Pamilo, P. (2005). Genetic population structure and dispersal patterns in Formica ants — a review. *Ann. Zool. Fennici*, *42*, 163–177.

Theunis, L., Gilbert, M., Roisin, Y., & Leponce, M. (2005). Spatial structure of litter-dwelling ant distribution in a subtropical dry forest. *Insectes Sociaux*, *52*, 366–377. https://doi.org/10.1007/s00040-005-0822-0

Tilman, D. (1994). Competition and Biodiversity in Spatially Structured Habitats. *Ecology*, *75*(1), 2–16. https://doi.org/10.2307/1939377

Tilman, D., May, R. M., Lehman, C. L., & Nowak, M. A. (1994). Habitat destruction and the extinction debt. *Nature*, *371*(6492), 65–66. https://doi.org/10.1038/371065a0

Travis, J. M. J., Delgado, M., Bocedi, G., Baguette, M., Bartoń, K., Bonte, D., Boulangeat, I., Hodgson, J. A., Kubisch, A., Penteriani, V., Saastamoinen, M., Stevens, V. M., & Bullock, J. M. (2013). Dispersal and species' responses to climate change. *Oikos*, *122*, 1532–1540. https://doi.org/10.1111/j.1600-0706.2013.00399.x

Wilson, C. J., & Jamieson, M. A. (2019). The effects of urbanization on bee communities depends on floral resource availability and bee functional traits. *PLOS ONE*, *14*(12), e0225852. https://doi.org/10.1371/journal.pone.0225852

Young, A., Boyle, T., & Brown, T. (1996). The population genetic consequences of habitat fragmentation for plants. *Trends in Ecology & Evolution*, *11*(10), 413–418. https://doi.org/10.1016/0169-5347(96)10045-8

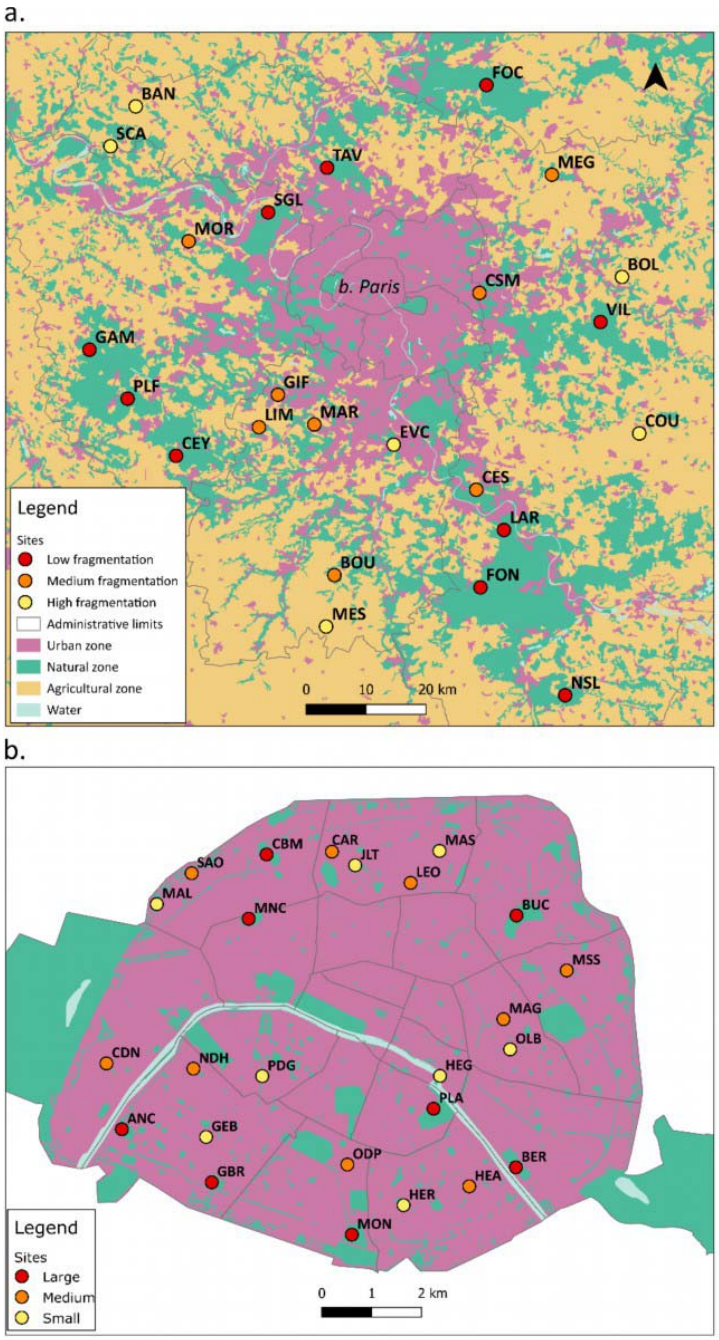

Figure 1: Map of the sampling sites in forests around Paris (Ile-de-France region) (a) and parks in Paris (b). The colour of the circles indicates the fragmentation level of forests or the size of parks. minimally fragmented forests (n = 10) have between 75 and 95% of forest cover within 1 Km, medium fragmented forests (n = 8) have between 30 and 70% of forest cover, and highly fragmented forests (n = 6) have less than 5% of forest cover in their surroundings. Parks are divided

based on surface: large (80 000 to 250 000 m^2 (n = 8)), medium (5 000 to 12 000 m^2 (n = 9)), and small (500-2 000 m^2 (n = 8)). Site information is detailed in Table S1.

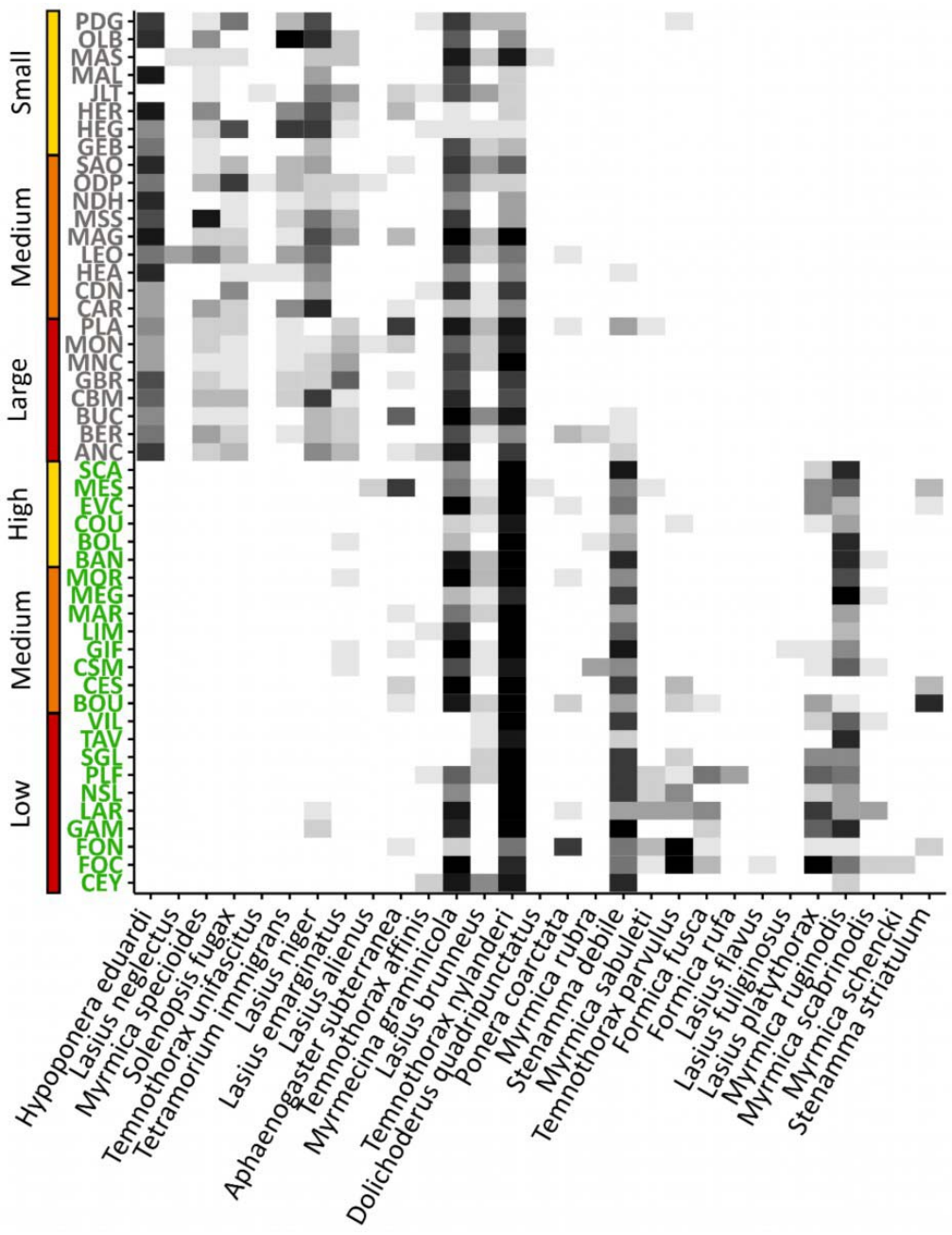

Figure 2: Variations in the presence and abundance of ant species depending on patches. Darker Levels show higher abundances, i.e., of the percentage of quadrats where the species was found. On the Y-axis, green patches correspond to forests and grey patches correspond to parks. Red, orange, and yellow show fragmentation levels for forests and patch sizes for parks. Species are ranked based on their urbanisation preference along the X-axis.

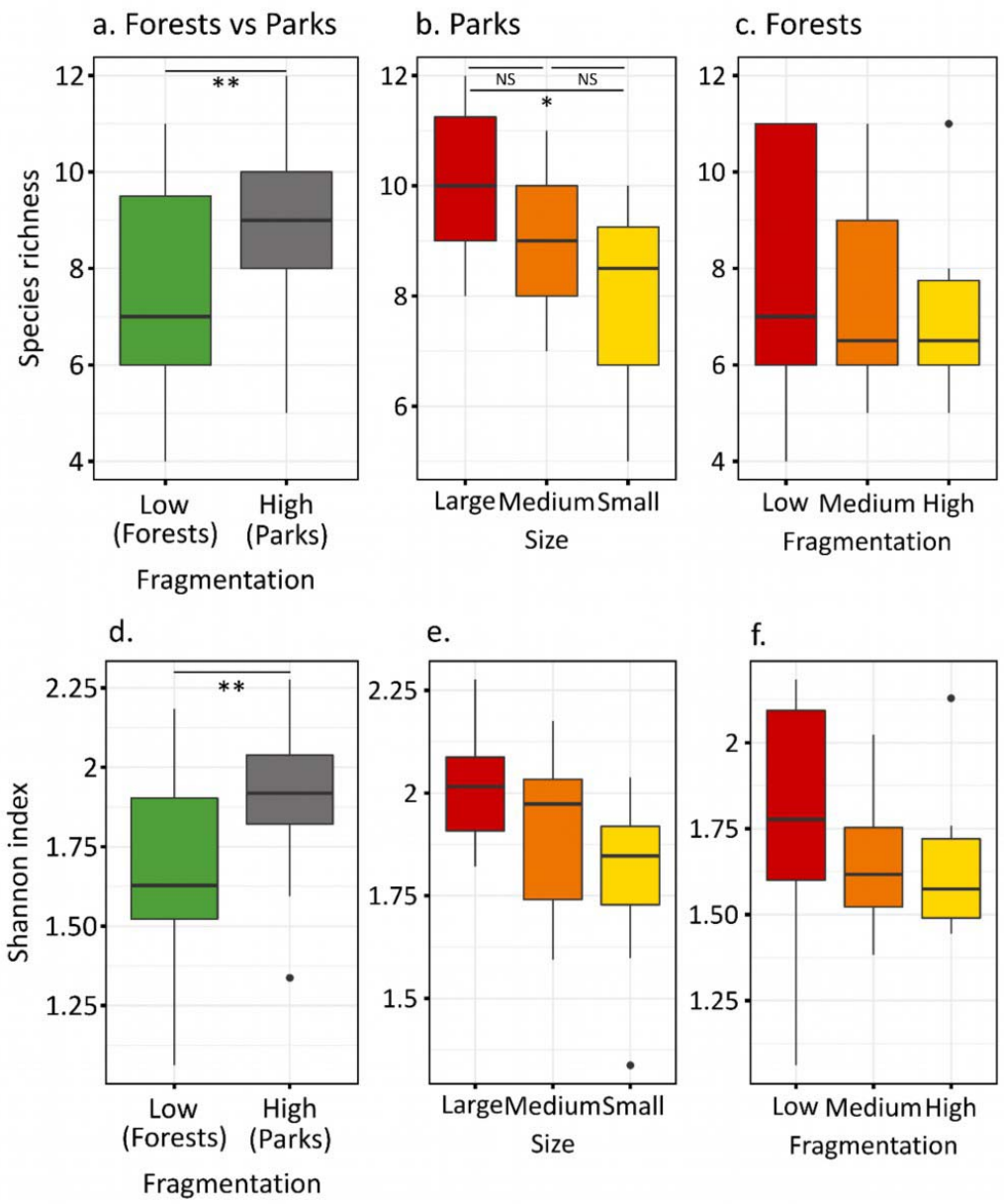

Figure 3: Species richness (a-c) and Shannon index (d-f) between forests and parks (a, d), between parks of different sizes (b, e), and between forests of different fragmentation levels (c, f). Significant differences are observed in species richness and Shannon index between forests and parks (Species richness: F value = 6.67, p = 0.013, R^2 = 10.6%; Shannon index: T value = 2.808, p = 0.007, R^2 = 13%), and in species richness between parks of different sizes (F = 3.74, p = 0.039, R^2 = 0.19).

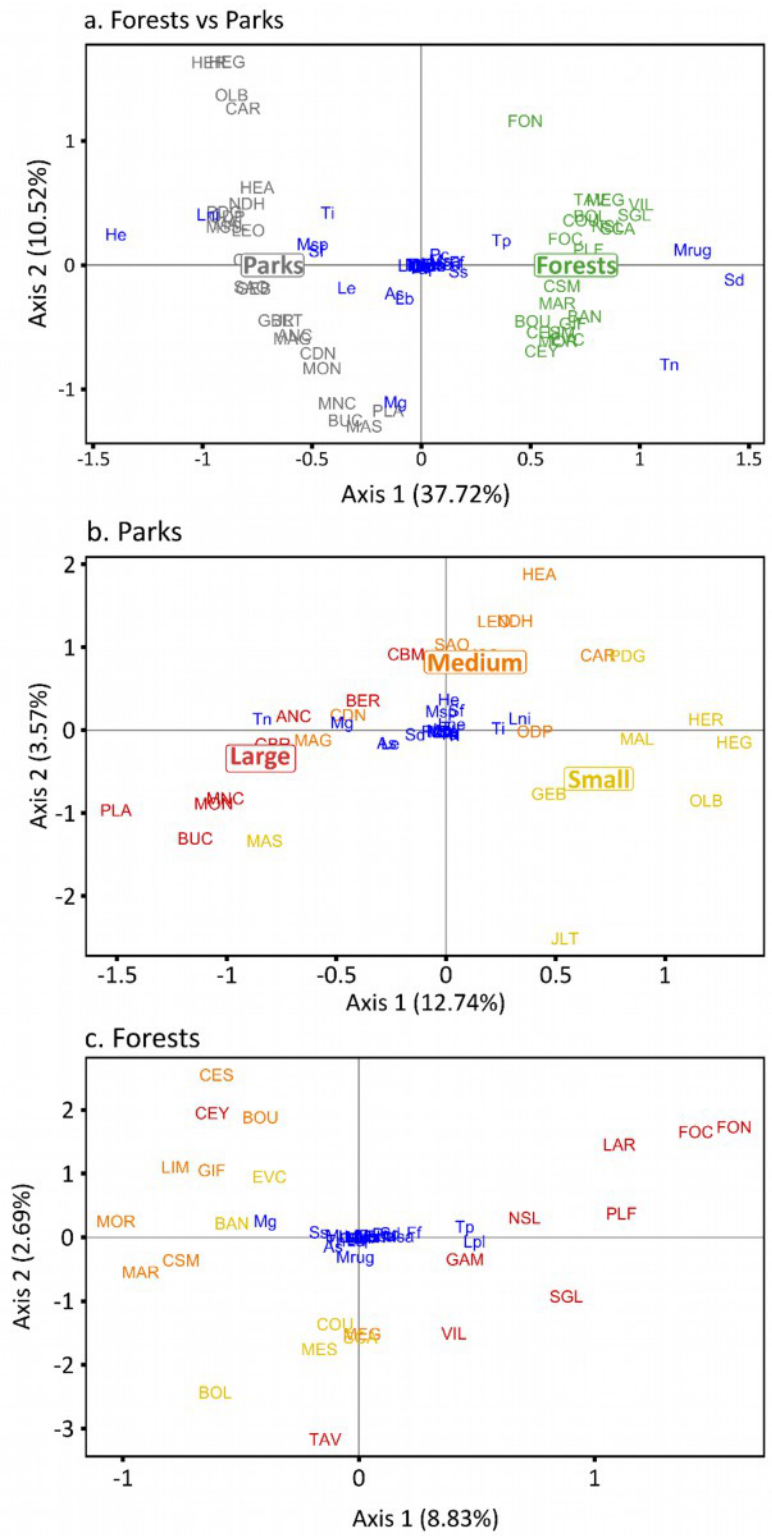

Figure 4: Beta diversity (db-RDA analysis) between forests and parks (a), between parks (b), and between forests (c). Blue acronyms are the species. Capital acronyms are the sites. For (c), yellow

represents high fragmentation, orange medium fragmentation, and red low fragmentation. Ant communities are markedly different between parks and forests, with communities from the two habitats being separated with no overlap (F value = 28.47, $p = 0.001$, $R^2 = 37.7\%$). Communities also clearly differ between parks of different sizes, with a gradual change in composition from small to medium to large parks (F value = 2.14, $p = 0.008$, $R^2 = 16.3\%$). No difference is observed between forests of different fragmentation level ($F = 0.77$, $p = 0.69$).

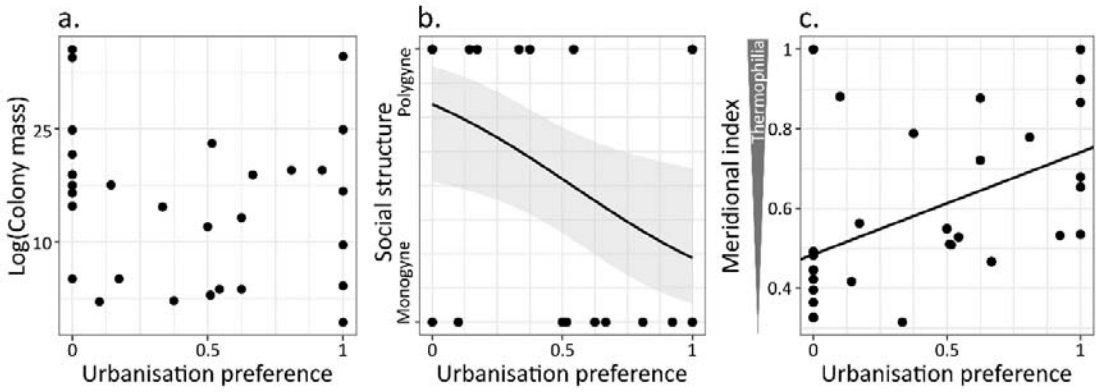

Figure 5: Relation between urbanisation preference of the species and their traits: colony mass (a), Social structure (b), Meridional index as a proxy of thermophily (c). Urbanisation preference varies between zero for strictly forest species to one for strictly urban species. It is correlated to the social structure (z value = -2.26, p = 0.02, R^2 = 0.15) and thermophily (t value = 2.89, p = 0.008, R^2 = 0.21), but not to the mass of the colony (t value = -0.76, p = 0.46).

692