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

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Abstract:

Environmental changes such as urbanisation and habitat fragmentation profoundly impact ecological communities. We investigated the response of ant communities to urbanisation and habitat fragmentation in the Paris region, comparing urban parks vs 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, i.e. seem little impacted by fragmentation, while park communities differ noticeably depending on park size, with larger parks harbouring more species. Our findings suggest that urbanisation selects specific ant traits favouring more thermophilic species, thereby increasing the mean thermal preference of urban communities. Such selective effects constrain spatial dynamics at the metacommunity level, with important implications for their maintenance in a climate change context.

Keywords: urbanisation, ants, metacommunity, trait selection, heat island effect, local adaptation

Introduction

Rapid urbanisation stands as a primary driver of biodiversity decline, exerting manifold impacts on ecosystems worldwide (Alberti 2015; Aronson *et al.* 2014; Diamond & Martin 2021; Johnson & Munshi-South 2017; Piano *et al.* 2020). This transformative process reshapes environments in many ways, fostering novel ecological dynamics and posing significant challenges to native flora and fauna. First, urbanisation 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. Second, 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.* 2016; McGlynn *et al.* 2019). This thermal gradient can influence species distributions, phenology, and physiological processes, driving community composition and structure shifts.

Given these rapid spatial environmental variations, marked local changes in species composition are expected, but they ultimately depend on the dispersal limitation of species making the community. Importantly, urbanisation is most often associated with high habitat fragmentation (Haddad *et al.* 2015). 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 *et al.* 2024b; 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).

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

Insects and in particular ants have an important impact on ecosystems by dispersing seeds, pollinating, participating in nutrient cycles, structuring the soil, and participating in food chains (Hölldobler & Wilson 1990). They are a very good model group to study the effects of urbanisation and habitat fragmentation on communities. First, their life history traits are variable between species. Some of these traits are strongly related to their dispersal abilities (size of individuals, presence or absence of wings) and competitiveness (size of colonies, diet), therefore playing a key role in which are key traits in metacommunity dynamics. Second, ants are abundantly present and diverse in and outside cities, which allows direct comparative studies. Most ant species depend on green spaces, which makes the city a very fragmented habitat compared to the countryside, even if some species can live in built areas. Last, they are easy to sample. Several empirical studies have shown that urbanisation and habitat fragmentation affect the species richness of ants, with a decrease in species richness as urbanisation increases and a change in community composition (Carpintero & Reyes-López 2014; Ješovnik & Bujan 2021; Leal *et al.* 2012; Pacheco & Vasconcelos 2007; Theunis *et al.* 2005). For instance, climate and resource specialist ants are more sensitive to 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 urban parks within the city (Figure 1). Forests are considered lowly 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. 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). Lowly 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® Version 2.0 from the "National Institute of Geographic and Forest Information" of France (IGN, https://inventaire-forestier.ign.fr/carto/afficherCarto/V2, last visit: 19/07/2022) to assess forest cover. Forest classes are evenly distributed around Paris, and we chose well-separated locations that likely represent independent plots (mean distance = 52.1 +/- 23.7 Km, min = 6.4 Km, max = 122.1 Km).

Parks fragmentation was measured using two metrics, size and isolation. We selected parks (n = 25) of three size classes (Figure 1b), namely large (n = 8, 80 000-250 000 m²), medium (n = 9, 5 000-12 000 m²), and small parks (n = 8, 500-2 000 m²), and measured their isolation as the quantity of green area (other parks) within 1 Km around the focal park boundaries. As for forests, we selected parks that were evenly distributed within Paris and well separated, assumed to represent independent points (mean distance = 4.9 +/- 2.1 Km, min = 552 m, max = 9.5 Km).

155 *Sampling*

156 We sampled forests between May and July 2020, between 11 am and 4 pm, on rainless days.
157 We distributed 12 quadrats of one square meter each, equally spaced every 9 m, along a transect of
158 100 m. We independently collected the litter and superficial soil on each of the 12 quadrats. We
159 collected organisms using the Winkler extraction method (Agosti *et al.* 2000). We detail the procedure
160 below.

161 We sampled parks between May and August 2021, between 11 am and 4 pm, on rainless days.
162 To compare the same ant communities in forests and parks, we targeted park areas with litter for
163 sampling, i.e. areas under trees or shrubs. We purposefully placed the 12 quadrats into these areas
164 and dispersed the quadrats within parks as much as possible (considering the configuration of the
165 parks, transect was not possible). One park (OLB) was so small that only five quadrats could be placed
166 and sampled, and owing to a disturbance only ten quadrats were sampled in another park (MAS). The
167 sampling and extraction protocols were the same for parks and forests.

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

176 While we sampled litter ants in forests and parks in two separate years (2020 and 2021) due
177 to logistical constraints, note that ant queens and colonies live several years and that the sampling
178 was done during the same season. We therefore assume that the year of sampling likely had little
179 effect and our data allows testing the effect of urbanisation and fragmentation.

180

181 *Identification of ant species*

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

186 *Ant species traits*

187 We selected different species-level traits to test for the effect of urbanisation. Queen size,
188 worker size and colony size (number of individuals) were obtained from the bibliography for all
189 collected species (Blatrix *et al.* 2013; Seifert 2018). In addition, colony mass was estimated as worker
190 size^3 X colony size. Because colony mass is directly linked to metabolic requirements (Brown *et al.*
191 2004), we expect that it could vary between urban and forest sites, either due to changes in resources
192 or temperature regimes.

193 We also analysed the social structure of a colony, with two levels: monogyny (species with
194 typically one queen per colony) and polygyny (species with typically several queens per colony). This
195 trait is to some extent linked to dispersal as monogynous species often perform independent colony
196 foundation (long dispersal distance strategy but low competitivity) whereas polygynous species do
197 colony fission (short dispersal distance strategy but high competitivity) (Cronin *et al.* 2013; Keller
198 1991).

199 Finally, for each species, we estimated thermophily based on a meridional index from
200 Daufresne et al. (2004). Species were considered meridional if most of their distribution lies south of
201 Paris, with meridionality being calculated by (Paris latitude – minimum observed latitude) / (maximum
202 observed latitude – minimum observed latitude). The meridional index for a given species is,
203 therefore, close to one when Paris is at the northern limit of its distribution, and close to zero when

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

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

215 *Analyses*

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

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

225 We analysed beta diversity with Jaccard's dissimilarity index because we here focus on species
226 presence/absence rather than on abundance. Direct use of individual densities could be problematic,
227 as our sampling procedure can recover isolated individuals as well as whole colonies. 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, 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 to each trait, we performed ANOVAs. 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).

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

Effect of park size

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

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

Effect of urbanisation on species traits

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

Discussion

Our study shows that urbanisation and the associated habitat fragmentation influence the litter ant communities at the metacommunity scale. Surprisingly, the ant biodiversity assessed by the total number of species per environment (gamma diversity) is stable and the species richness per patch is slightly higher in parks than in forests. Community compositions differ markedly between the two environments, with a strong turnover in species. 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.

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

300 dominated by its turnover component. This suggests that dispersal is low between the two
301 environments, creating different communities adapted to each, and highlights species sorting as a
302 strong regional scale mechanism in this metacommunity. Indeed, if dispersal between forest and
303 urban sites was high, we would expect either community composition to be similar (low beta diversity)
304 or, if colonization success differed between the environments, that the communities of one
305 environment would be a subset of the communities of the other environment (high nestedness,
306 Baselga 2010).

307 Surprisingly, more species are present per urban park than per forest. Several explanations
308 can be proposed. First, as mentioned above, species sorting dominates suggesting restricted dispersal
309 between forests and city parks, and parks may thus host more ant species than forests if they harbour
310 a higher diversity of habitats and microenvironments. This hypothesis would implicitly question our
311 view of forests being good patches compared to parks. Another possibility would be that forests are
312 (or have been until relatively recently) well-connected and form a metacommunity of their own. If so,
313 high dispersal among forests could homogenise ant forest communities through mass effects, leading
314 to a depressed lower alpha diversity reflecting partial homogenization (Leibold *et al.* 2004; Mouquet
315 & Loreau 2003). In contrast, when dispersal is low, as may be the case between parks, competition
316 occurs independently within each park resulting in different communities hence higher alpha and
317 gamma diversities. This increases turnover between patches as observed in our data. This is likely
318 given that parks were made for human leisure and differ more from one another than natural forests
319 do.

320 Our observations of local community compositions support the idea of strong mass effects
321 among forests. Indeed, there is no difference in species richness and species composition among
322 forests, even for the most fragmented ones. This suggests a high degree of dispersal between forest
323 sites, which homogenises the communities. This is plausible because the matrix separating forests is
324 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. Although, this should 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.

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

351 Beyond the turnover in species composition, we highlight that phenotypic traits are
352 deterministically associated with community variations. Urban species are more often monogynous
353 and more thermophilic. While the second trait was expected, given the heat island effect in cities, the
354 first was not. Monogyny is somewhat linked to dispersal capacity (Keller 1991; Sundström *et al.* 2005).
355 Winged queens disperse alone by flying over long distances and hence typically found monogynous
356 colonies. In contrast, apterous queens disperse on foot over short distances with workers, and in some
357 cases with related queens with whom they found polygynous colonies. Theoretically, habitat
358 fragmentation can select for high dispersal (i.e. winged queens), for instance when dispersal is traded-
359 off with competition capacity (Finand *et al.* 2024b; Tilman 1994), when fragmentation leads to high
360 kin competition in remaining patches, or to avoid inbreeding (Cote *et al.* 2017; Gandon 1999; Hamilton
361 & May 1977). Some empirical studies support these theoretical results, including in ants. For instance,
362 at the intraspecific level colonisation ability can be in a trade-off with competition in an ant species
363 (Finand *et al.* 2024a). This selection for high dispersal in a fragmented context could explain, as a
364 byproduct, that city parks harbour more monogynous species because polygynous species disperse
365 less. However, some studies have shown opposite results, with habitat fragmentation in cities
366 selecting for lower dispersal (Cheptou *et al.* 2008; Finand *et al.* 2023). Indeed, while habitat
367 fragmentation usually favours high dispersal, it may have the opposite effect under some
368 circumstances (e.g. highly hostile matrix increasing dispersal costs, Bonte et al. 2012; Hastings 1983).
369 A second explanation is that monogynous species can be considered as pursuing spatial bet-hedging
370 because flying queens can access and distribute the risks on more patches than walking queens.
371 Indeed, a colony producing flying queens can attempt to establish new colonies on many patches. In
372 contrast, a colony producing apterous queens produces a few only, as each requires the allocation of
373 workers, and they have restricted dispersal hence it has few establishment attempts. A bet-hedging
374 strategy is selected under temporally variable environments (Slatkin 1974). City patches may be more
375 variable, due to many disturbances associated with human activities, and parks surrounded by
376 unfavourable environments. Having winged queens will increase the probability of having offspring in

a more favourable environment. A third hypothesis is that urban parks are relatively new, particularly regarding ants that have a longer generation time than most other insects. The first species colonising a new patch are the most dispersive ones, which in ants have winged queens and thus are monogynous. Dispersal limitation also likely lasts in this highly fragmented context. Forests being much older, the less dispersive but more competitive species had the time to colonise them and progressively exclude better colonisers. All these hypotheses are not exclusive. Other taxa have shown this shift in community composition with more dispersive species in the city, like carabid beetles (Piano *et al.* 2017).

The high abundance of thermophilic ants in urban areas aligns with numerous studies indicating that cities, such as Paris, are subject to the Urban Heat Island effect (Lemonsu *et al.* 2015). Heat-susceptible species may disappear, and thermophilic species may dominate communities in cities. The prevalence of thermophilic species in urban areas has been documented not only in ants but also in other groups, such as carabid beetles (Piano *et al.* 2017) and moths (Franzén *et al.* 2020). More broadly, the process of thermophilisation, where communities shift toward species that prefer warmer conditions due to rising temperatures, has also been observed in non-urban ecosystems, including fish (Daufresne *et al.* 2004) and plants (Feeley *et al.* 2020). This result is particularly relevant in the context of climate change, as temperatures are expected to rise in the coming decades, leading to significant ecological consequences (McCarty 2001). Cities offer a valuable natural laboratory for studying the impacts of climate change, with urban communities serving as ideal experimental units to investigate these effects. Furthermore, our findings suggest that climate change could act as a critical filter for community composition, potentially leading to the decline of less thermophilic species. While urban areas might serve as reservoirs for future biodiversity under changing climates, they will likely become increasingly inhospitable for many species as climate change progresses.

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Conflict of interest:

The authors declare no conflict of interest.

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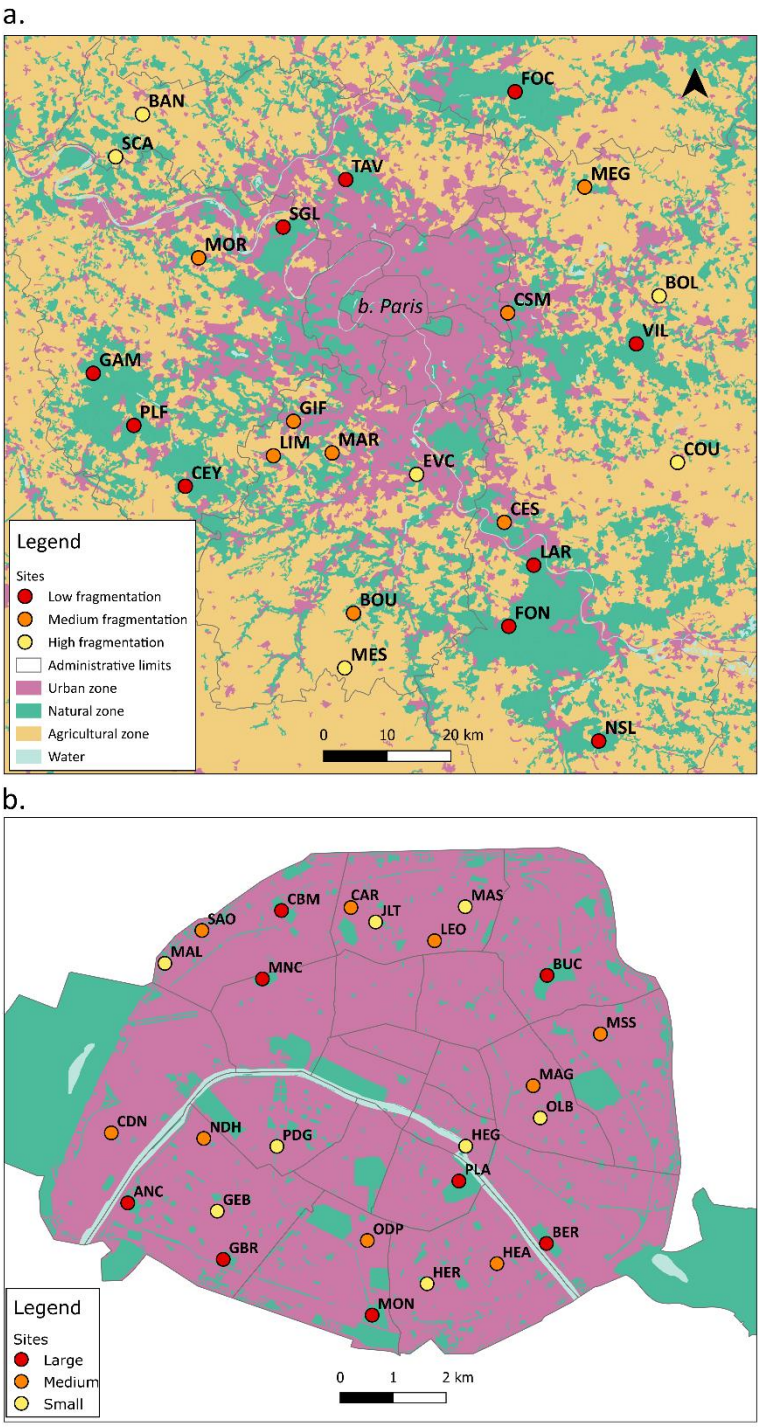

Figure 1: Map of the sampling sites in forests around Paris (Ile-de-France region) (a) and parks in Paris (b). The colour of the circles indicates the fragmentation level of forests or the size of parks. Lowly fragmented forests (n = 10) have between 75 and 95% of forest cover within 1 Km, medium fragmented 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 m² (n = 8)), medium (5 000 to 12 000 m² (n = 9)), and small (500-2 000 m² (n = 8)). Site information is detailed in Table S1.

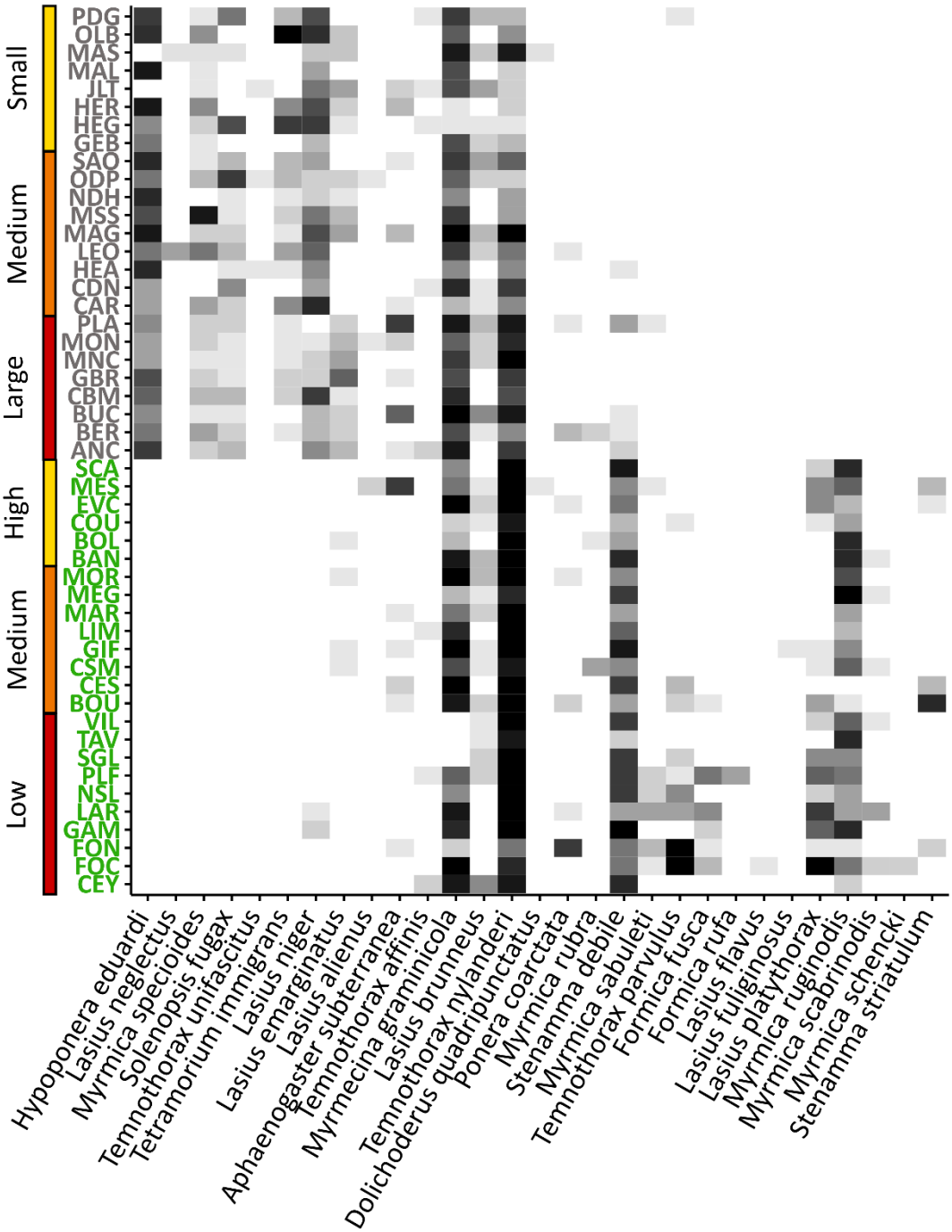

Figure 2: Variations in the presence and abundance of ant species depending on patches. Darker Levels show higher abundances, i.e., of the percentage of quadrats where the species was found. On the Y-axis, green patches correspond to forests and grey patches correspond to parks. Red, orange, and yellow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

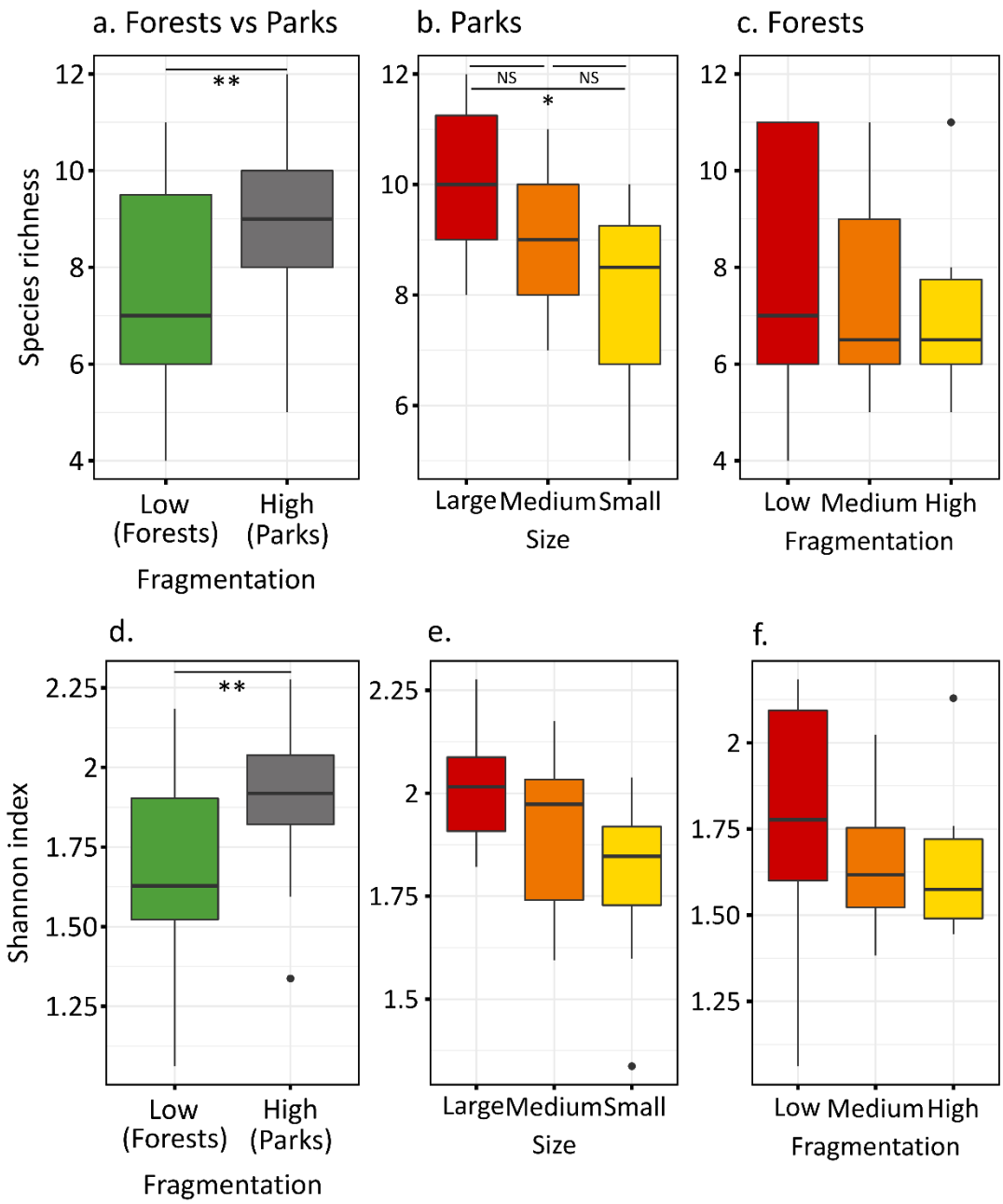

Figure 3: Species richness (a-c) and Shannon index (d-f) between forests and parks (a, d), between parks of different sizes (b, e), and between forests of different fragmentation levels (c, f). Significant differences are observed in species richness and Shannon index between forests and parks (Species 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).

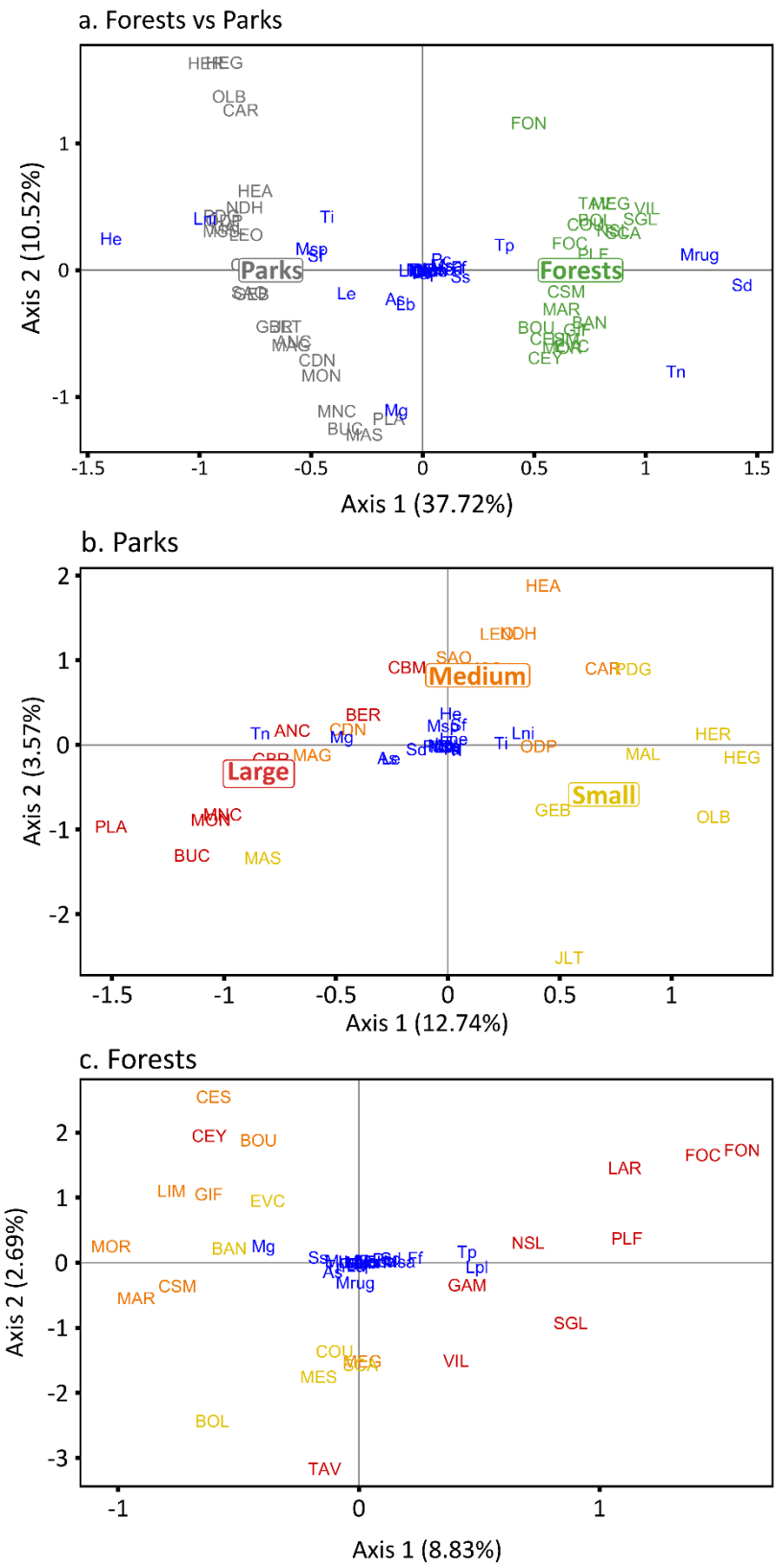

Figure 4: Beta diversity between forests and parks (a), between parks (b), and between forests (c). Blue acronyms are the species. Capital acronyms are the sites. Communities are different between

parks and forests (F value = 28.47, $p = 0.001$, $R^2 = 37.7\%$), between parks of different sizes (F value = 2.14, $p = 0.008$, $R^2 = 16.3\%$), but no difference is observed between forests of different fragmentation level (F = 0.77, $p = 0.69$).

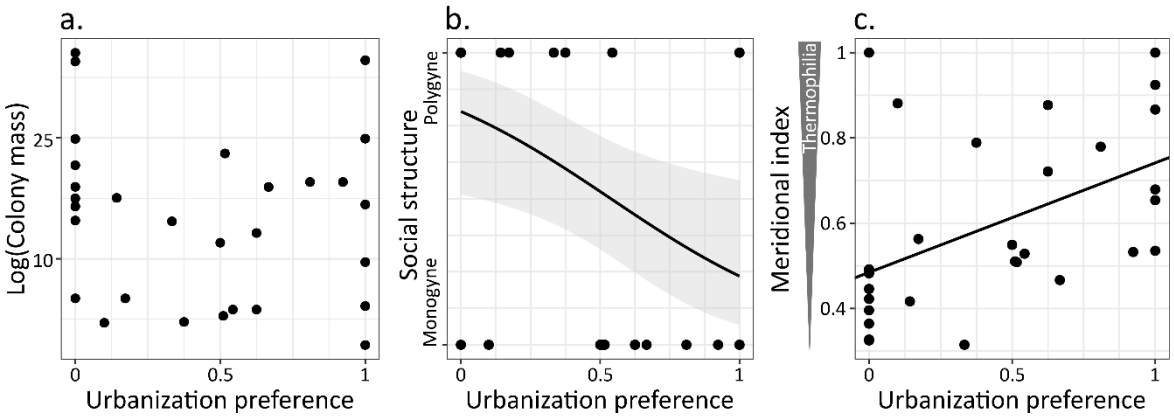

Figure 5: Relation between urbanisation preference of the species and their traits: colony mass (a), Social structure (b), Meridional index as a proxy of thermophily (c). Urbanisation preference varies between zero for strictly forestry species to one for strictly urban species. It is correlated to the 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).

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