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1 Segregation of floricolous ants along latitudinal and urbanization 2 gradients

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17

18 **Abstract**

19 Recent call has been made to study the biogeography of species interactions in order to better
20 understand ecosystems' states and processes, as well as their response to global anthropogenic
21 disturbances. Ants (Formicidae) are a dominant group of arthropods with a central role in
22 ecosystem functioning. Many ant species, those feeding on liquids, are floricolous and consume
23 nectar. The biogeography of ant-flower interactions is still poorly studied and especially in
24 temperate area. Here we quantify variations in ant-flower interaction frequency in response to
25 latitudinal and urbanization gradients at a country scale.

26 We used data from a flower-visitor monitoring program that includes pictures on 2511 flower
27 plants across Continental France (Mainland) and over 4 years. We analysed the occurrence of
28 the ant-flower interactions along two gradients: latitude and urbanization, this for 10 ant taxa
29 corresponding to different taxonomical level (from family to species).

30 Ants visited 26 % of the sampled plants. Most of the observed ant-flower interaction involved
31 the subfamily Formicinae (82.1 %), followed by Myrmicinae and Dolichoderinae (6.9 % and
32 4.6 % respectively). Globally, (i) the probability of occurrence was negatively related to
33 latitudes (ii) and to urbanization at lower latitude. (iii) Responses to latitude among sub families,
34 genus and species level responses were segregated and taxonomically aggregated.

35 At lower taxonomic levels we found clear latitudinal niche partitioning among ant taxa
36 suggesting that competition, on both evolutionary and ecological time scales, is a major process
37 structuring ant communities. Finally, our results highlight that the effects of large scale
38 perturbation like urbanization can vary and affect latitudinal gradient.

39 **Keywords:** Insect distribution; Urbanization; Formicidae; Functional biogeography; Citizen
40 Science; Inter-specific interaction; Niche partitioning

41

42

43 **Introduction**

44 A major aim of biogeography is to unravel the spatio-temporal distribution of species and
45 ecosystems as well as the underlying abiotic factors and biotic processes shaping such
46 distribution (Lomolino *et al.* 2006). This scientific field provided major insights for the
47 understanding of natural gradients such as the decrease of diversity with increasing latitude at
48 global scale (Gaston 2000, Rolland *et al.* 2014). There is growing evidence that global change
49 can act as an additional driver shaping such large-scale diversity patterns. Indeed, human
50 activities induce major environmental modifications such as climate or land use changes, with
51 consequences on both species distribution and the functioning of species assemblages (Sala *et*
52 *al.* 2000, Tylianakis *et al.* 2008). Understanding how such natural and human induce drivers of
53 species distribution interact appears as one of the current challenges of biogeography (Parmesan
54 *et al.* 2005).

55 Here we propose to address this challenge investigating the combined effects of latitude and
56 urbanization on the distribution of the interaction between liquid-feeding ants and flower plants
57 across Continental France.

58 Urbanization represents the prime driver of land use change in Europe (EEA 2010), with city
59 areas increasing at a high rate and projected to double by 2030, reaching 6 % of emerged earth's
60 surface (Banque_Mondiale 2009). Urbanization has consequences far beyond cities'
61 boundaries and impacts biodiversity patterns at a large scale (Pickett *et al.* 2011) mainly causing
62 an impoverishment of communities and increasing the dominance of few urbanophile species
63 (McKinney 2006).

64 For ants, most studies showed a negative effect of urbanization on species richness (Antonov
65 2008, Antonova and Penev 2006, Forys and Allen 2005, Holway and Suarez 2006, Lessard and
66 Buddle 2005, López-Moreno *et al.* 2003, Majer and Brown 1986, Sanford *et al.* 2009,
67 Thompson and McLachlan 2007, Uno *et al.* 2010, Xu *et al.* 1998) and one study a positive
68 effect (Ives *et al.* 2011). The effects of urbanization on ant's abundance have been less studied

69 and showed a more contrasted pattern (Antonova and Penev 2006, Buczkowski and Richmond
70 2012, Sanford *et al.* 2009, Uno *et al.* 2010). Indeed, rare species seem to exploit the
71 modifications induced by urbanization and can reached high densities in cities (McKinney
72 2008, Vepsäläinen *et al.* 2008). To our knowledge, only one study has investigated the response
73 of ant-plant interaction (Thompson and McLachlan 2007) which highlighted an increase of
74 seeds' removal rate by the few species that remained in more urbanized forest.

75 Ants (Hymenoptera, Formicidae) are among the most abundant and ecologically significant
76 groups on earth, sometime referred then as “the little things that rule the world” (Hölldobler
77 and Wilson 1990), as they can deeply modify the environment, to the point of being considered
78 as ecological engineers (Jones *et al.* 1994). As suggested by the correlated pattern of
79 diversification between ants and angiosperm (Moreau *et al.* 2006), the interactions establish by
80 ants with flowering plants might have been key to their current widespread distribution (Rico-
81 Gray and Oliveira 2007). Their distribution varies along latitudinal gradient (Baroni Urbani and
82 Collingwood 1977) and so their taxonomic diversity at both global (Dunn *et al.* 2009, Jenkins
83 *et al.* 2011) and local scales (Del Toro 2013, Segev 2010).

84 Ant-plant interactions are diverse and distributed along an antagonism-mutualism continuum,
85 with some ants feeding directly or indirectly on plants, inhabiting plants, protecting plant
86 against herbivory, dispersing seeds, and even pollinating plants (Rico-Gray and Oliveira 2007).
87 For species referred as liquid-feeding, which are frequent flowers visitors, consumer-resource
88 interactions seem dominant. They often directly feed on plants, either from extrafloral nectary
89 (Rico-Gray and Oliveira 2007) or within flowers (Herrera *et al.* 1984). Another explanation for
90 the presence of ants on flowers is the mutualistic association between some ants and aphids.
91 Indeed, many liquid-feeding ants plants have developed trophobiotic relationships with
92 homopterous (aphids, coccids, membracids or lycaenids) and collect honeydew, such as the
93 workers of the subfamilies Formicinae and Dolichoderinae and a few species in the genus

94 *Myrmica* and *Tetramorium* of Myrmicinae (Stadler and Dixon 2005). While protecting aphids
95 from potential parasitoids and predators they often patrol on flowers.
96 Using a large dataset coming from a citizen science program monitoring flower visitors across
97 Continental France, we proposed to analyze the combine effect of latitude and urbanization on
98 the presence of ants on flowers. According to spatial scale and taxonomic hierarchy, latitudinal
99 gradients of biodiversity can show various patterns (Gaston 1996, Willig *et al.* 2003) : from
100 positive to negative linear relationships, but also quadratic or non significant ones. In France,
101 for example, Lobo *et al.* (2002) showed a quadratic relationship of dung beetles occurrences.
102 We test whether ants' response to latitude is linear or quadratic and to what extent such
103 latitudinal response is affected by urbanization. We carry out our analysis at various taxonomic
104 levels, from family to species, looking for similarities and singularities in these responses.

105 **Material and Methods**

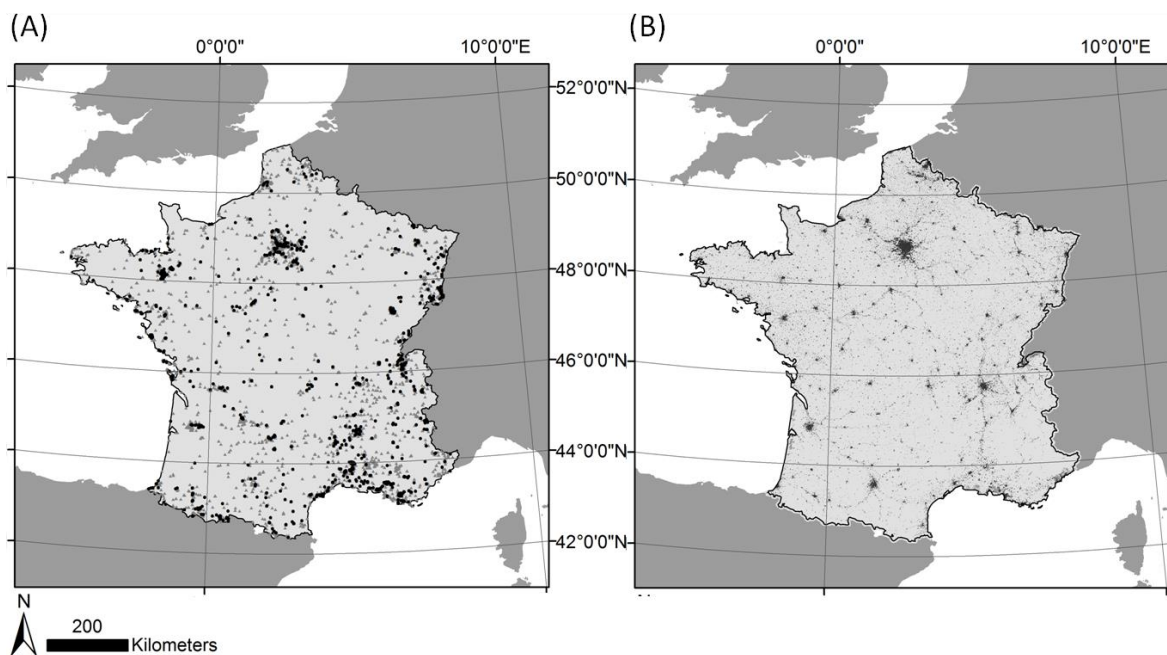
106 **1. Studied area**

107 The study took place across Mainland Continental France (here after France), spanning a
108 latitudinal gradient from 51.08° to 42.32° N (Fig. 1). It covers an area of 675,000 km².

109 **2. The dataset**

110 Data comes from a citizen science program aiming at monitoring flower visitor across France
111 using a standardized protocol fully described elsewhere (Deguines *et al.* 2012). Briefly,
112 volunteers choose a flowering plant anywhere in France and take pictures of every insect
113 visiting its flowers within a 20-minute period. Then, insects and plant pictures are identified
114 using online computer-aided identification tools (Causse *et al.* 2013) that propose sets of
115 predefined taxa or morphospecies, including one “ant” taxa. The date, time, temperature and
116 precise location of the observations are provided by volunteers when uploading their data on
117 the program website (www.spipoll.org). Each set of identified plant and insects visiting it at a

118 given time and place is referred as a collection. For the purpose of the present study, we used
119 all the collections recorded from 2010 to 2014 that comprised a total of 14,027 collections
120 including 2518 picture of ants (Fig 1. A). They spanned a latitudinal gradient from 42.36° to
121 51.06°N and covering more than 99 % of France latitudinal gradient. All ant pictures were then
122 identified to the highest taxonomic resolution possible by professional experts. S1 Table in
123 Supporting Information detailed these taxonomic groups, ranging from the family to the species
124 level.



125
126 **Fig 1. Locations of collections and urbanization in Continental France.** In both maps,
127 Continental France is represented in light grey and the other emerged areas are represented in
128 dark grey. (A) Collections with ant are represented by black dots and without by grey triangles.
129 (B) Urbanized areas are represented in black and other land uses in light grey.

130 3. Urbanization index

131 Urbanization was characterized by the artificial area category of the first level of Corinne Land
132 Cover 2006 database (raster version 25 m resolution, EEA 2010). In France, urbanization is

133 positively correlated with latitude (EEA 2006). To disentangle the potential urbanization and
134 latitude effects, we followed the methodology proposed by Deguines *et al.* (Deguines *et al.*
135 2012) and calculated a relative urbanization index. Precisely, for each collection, we first
136 measured the proportion of urban land use within a 1 km radius. Then, for each collection we
137 subtracted to this proportion the mean proportion of urban land use within a 1 km radius of all
138 the collection located within a 100 km radius of the focal collection. This index of relative
139 urbanization is thus positive when the focal collection is more urbanized than the collections
140 that have been sampled regionally (i.e. within a 100 km radius) and negative when the focal
141 collection is less urbanized than the collection sampled regionally. Seven Collections that
142 presented less than 30 other collections in the 1 km radius where excluded from the analysis.

143 **4. Statistical Analysis**

144 We analysed the presence/absence of the nine most abundant ant taxonomic groups within the
145 collections using generalised linear models with binomial error distribution. We included as
146 explanatory variables in the model the latitude of the collection, its index of relative
147 urbanization and the interaction between both. To allow for quadratic response to latitude, we
148 also included the squared latitude and its interaction with the index of relative urbanization. All
149 models were simplified to the minimum adequate models based on the Akaike Information
150 Criterion (Johnson and Omland 2004). Significant of parameters was obtained with an Anova
151 type 3 test.

152 **Results**

153 **1. Identity of floricolous ants**

154 Flower visiting ants were present in 17.9 % of the 14,027 collections included in our dataset,
155 totalising 2511 ant observations. We specified the identification of 92 % of these observations
156 to a level ranging from subfamily to species (Table 1 and S1).

157 **Table 1. Occurrences of the 10 taxa studied.**

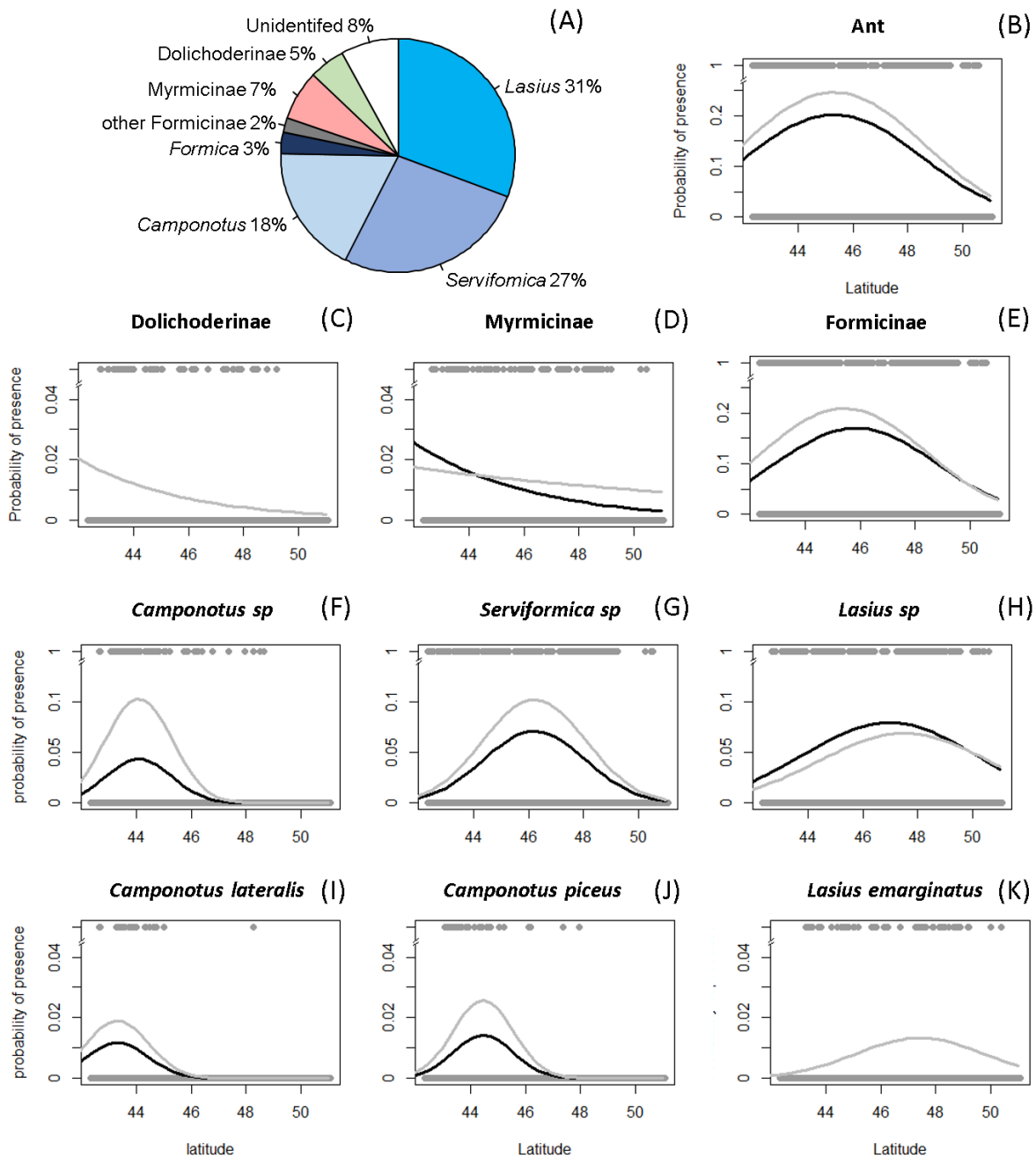
Taxa levels			
family	subfamily	Genus	Species
Ants (Formicidae, 2511)	Dolichoderinae (116)		
	Formicinae (2061)	<i>Camponotus</i> (464)	<i>Camponotus lateralis</i> (Olivier, 1792) (76)
			<i>Camponotus piceus</i> (Leach, 1825) (120)
		<i>Lasius</i> (781)	<i>Lasius emarginatus</i> (Olivier, 1792) (116)
		<i>Serviformica</i> (697)	
	Myrmicinae (174)		

158 *Authority are given for species level*

159 This revealed that floricolous ants were not evenly distributed among subfamilies: 81 %
 160 belonged to Formicinae, 7 % to Myrmicinae and 5 % to Dolichoderinae (Fig 2 (A)). The
 161 remaining 8 % of ant picture were not good enough to attribute them to a subfamily. Within
 162 Formicinae, three genera were highly dominant: *Lasius*, *Serviformica* (subgenus of *Formica*)
 163 and *Camponotus* that represented respectively 31 %, 27 % and 18 % of all ant observations (Fig
 164 2 (A)). Within these genera, we were further able to identify three species: *Lasius emarginatus*,
 165 *Camponotus piceus* and *Camponotus lateralis* that represented respectively 4.6 %, 4.7 % and
 166 3.0 % of all identified ants.

167 **2. Responses to latitudinal and urbanization gradients**

168 When analysing the distribution of ant observations across France, we found a significant
 169 quadratic effect of the latitude indicating a hump-shaped response of ant presence with an
 170 optimum around 45-46 °N (Fig 2 (B) and Table 2). We further found a significant interaction
 171 between the latitude and the index of relative urbanization indicating that urbanization affected
 172 ant presence differently along the latitudinal gradient, with a negative effect at lower latitude
 173 (Fig 2 (B) and Table 2).



174

175 **Fig 2. Pie chart of the relative presence and probability of presence along latitudinal and**
 176 **urbanization gradients of the nine taxa studied.** (B to K) Lines represent prediction from
 177 generalized linear models similar to the ones presented in the methods except that the relative
 178 urbanization effect was treated as a factor with two levels: low (grey) and high (black), each
 179 corresponding to half of the collections with respectively the lowest and highest values of
 180 relative urbanization.

181

182 The analysis of the presence of the three ant subfamilies highlighted striking differences among
183 them. First, Formicinae subfamily exhibited a pattern similar to the one observed for all the
184 ants, with a significant quadratic effect of the latitude with an optimum around 45-46 °N, and
185 a significant interaction between the latitude and the index of relative urbanization showing a
186 negative impact at low latitude (Fig 2 (E) and Table 2). Second, Myrmicinae subfamily
187 exhibited a significant interaction between the latitude and the index of relative urbanization
188 highlighting a positive impact at low latitude and a negative impact at high latitude (Fig 2 (D)
189 and Table 2). Finally, for Dolichoderinae subfamily, we found a significant effect of the latitude
190 (Table 2) revealing a steady decrease in the presence of this subfamily with increasing latitude
191 (Fig 2 (C)).

192 Scaling down our analysis at the genus level, we found a significant quadratic effect of latitude
193 for the three main genera belonging to Formicinae subfamily (Table 1). Interestingly, the
194 optimum was different for each genus. While *Camponotus* appeared to be the most southern
195 genus with a presence peak around 44 °N, the optimum for *Serviformica* was around 46 °N and
196 *Lasius* appeared to be the northernmost genus with its optimum located between 46 and 48 °N
197 (Fig 2 F, 2 G and 2 H, respectively). The presence of these three genera was also significantly
198 affected by the level of relative urbanization, but slightly differently. For *Serviformica* and
199 *Camponotus* genus, we found a significant negative effect of the relative urbanization (Fig 2
200 (F) and 2 (G) and Table 2). For *Lasius*, we found a significant interaction between the relative
201 urbanization and the latitude indicating that the effect of urbanization was dependent on the
202 latitude, with a positive effect for intermediate latitudes (between 45-47 °N) (Fig 2 (H) and
203 Table 2).

204

205

206

207

208 **Table 2. Minimum adequate models for each of the nine ant groups.**

		Ant (Formicidae)				Formicinae		
Terms	Df	Estimate (Std)	Chisq	P value	Estimate (Std)	Chisq	P value	
Latitude	1	5.59 (0.59)	95.94	<1.0E-4	6.51 (0.65)	110.02	<1.0E-4	
Urbanization	1	-0.01 (0.001)	36.71	<1.0E-4	-0.06 (0.02)	8.7	0.003	
Latitude ²	1	-0.06 (0.01)	99.79	<1.0E-4	-0.07 (0.01)	112.86	<1.0E-4	
Latitude x Urbanization	1				0.001 (4.4E-04)	7.46	0.006	

		Myrmicinae				Dolichoderinae		
Terms	Df	Estimate (Std)	Chisq	P value	Estimate (Std)	Chisq	value	
Latitude	1	-0.15 (0.04)	16.68	<1.0E-4	-0.26 (0.05)	30.58	<1.0E-4	
Urbanization	1	0.15 (0.06)	6.33	0.012				
Latitude ²	1							
Latitude x Urbanization	1	-0.003 (0.001)	6.72	0.01				

		Serviformica				Camponotus		
Terms	Df	Estimate (Std)	Chisq	P value	Estimate (Std)	Chisq	P value	
Latitude	1	14.57 (1.23)	171.97	<1.0E-4	32.43 (4.08)	122.02	<1.0E-4	
Urbanization	1	-0.01 (0.003)	25.58	<1.0E-4	-0.02 (0.002)	68.47	<1.0E-4	
Latitude ²	1	-0.16 (0.01)	172.26	<1.0E-4	-0.37 (0.05)	128.25	<1.0E-4	
Latitude x Urbanization	1							

		Lasius				Lasius emarginatus		
Terms	Df	Estimate (Std)	Chisq	P value	Estimate (Std)	Chisq	P value	
Latitude	1	5.31 (0.94)	34.09	<1.0E-4	8.87 (2.6)	13.575	<1.0E-4	
Urbanization	1	0.06 (0.03)	4.41	0.036				
Latitude ²	1	-0.06 (0.01)	32.95	<1.0E-4	-0.09 (0.03)	13.068	<1.0E-4	
Latitude x Urbanization	1	-0.002 (4.6E-4)	3.85	0.05				

		Camponotus lateralis				Camponotus piceus		
Terms	Df	Estimate (Std)	Chisq	P value	Estimate (Std)	Chisq	P value	
Latitude	1	35.17 (15.45)	10.21	0.002	38.75 (7.82)	50.881	<1.0E-4	
Urbanization	1	-0.01 (0.01)	4.3	0.038	-0.01 (0.005)	8.561	0.003	
Latitude ²	1	-0.41 (0.18)	10.21	0.001	-0.44 (0.09)	52.702	<1.0E-4	
Latitude x Urbanization	1							

209 For each group, the selected model was composed of the terms with Estimates, Chi-square
 210 values and p-values.
 211

212 Scaling further down our analysis to the three species we could identify and with sufficient data
 213 (S1 appendix), we found a significant quadratic effect of latitude for each one. As for the three
 214 genera analysed above, we found that the optimum varied among species: *Camponotus lateralis*
 215 appeared to have the southernmost distribution, peaking around 43.5 °N (Fig 2 (I)), followed

216 by *Camponotus piceus* that peaked between 44 and 44.5 °N (Fig 2 (J)). *Lasius emarginatus* had
217 the most northern and spread out distribution that peaked around 47.5 °N (Fig 2 (K)). While the
218 level of relative urbanization did not affect *Lasius emarginatus* (Fig 2 (K)), we found a
219 significant negative effect of the relative urbanization for *Camponotus lateralis* (Fig 2 (F) and
220 Table 2) and *Camponotus piceus* (Fig 2 (J) and Table 2).

221

222 **Discussion**

223 **1. Dominance of Formicinae on flowers**

224 At the subfamily level, almost 80 % of the observed floricolous ants belonged to Formicinae
225 subfamily. This result is consistent with Rico-Gray and Oliveira (Rico-Gray and Oliveira 2007)
226 that considered Formicinae as one of the most floricolous subfamily which could be explained
227 by the liquid-feeding (flower nectar or honeydew from aphids) behaviour of most species.
228 Surprisingly, ants from the subfamily Dolichoderinae, which is also considered as highly
229 floricolous (Rico-Gray and Oliveira 2007) were observed in 5 % of the collections only. This
230 overall low occurrence could be explained by the mainly southern distribution observed; this
231 pattern is consistent with what is known of the distribution of this subfamily (Blatrix *et al.*
232 2013). Turning to Myrmicinae, their low occurrence in our dataset is consistent with their more
233 predators and less floricolous habits than the two previous subfamilies (Rico-Gray and Oliveira
234 2007). Finally, the negligible occurrences of the last three subfamilies present in France, the
235 Ponerinae, (less than 0.1 %), none of the Leptanillinae nor the Proceratiinae is again consistent
236 with their almost strict edaphic behaviour in Continental France (Bernard 1968, Blatrix *et al.*
237 2013).

238 **2. Match and mismatch with known species latitudinal distribution**

239 Most of the knowledge about ant distribution is at the species level. Two of the three ant species
240 with sufficient data to analyse their latitudinal distribution on flower showed a good match

241 between the distribution we observed and their known latitudinal species distribution. Indeed,
242 the narrow and southern range we observed for *C. lateralis* is consistent with Blatrix *et al.*
243 (2013) that consider this species as absent or very rare above 46 °N. Similarly, the wide
244 latitudinal range of *L. emarginatus* we observed on flowers is consistent with its known
245 presence all over Continental France (Blatrix *et al.* 2013).

246 Interestingly presence on flowers of *C. piceus*, the last ant species with enough data to analyse
247 its latitudinal distribution, was observed on a much narrower latitudinal range than its known
248 distribution (between 43-50 °N, Blatrix *et al.* 2013). For ants, inter-specific competition is
249 considered as the major driver of community composition (reviewed by Cerdá *et al.* 2013) and
250 especially competition for food resources (Albrecht and Gotelli 2001, Blüthgen and Fiedler
251 2004, Lester *et al.* 2010, Vepsäläinen and Pisarski 1982). Vepsäläinen and Pisarski (1982)
252 divided species in three levels of hierarchy based on their respective dominance in
253 communities: (1) dominants that compete and exclude other species from territory and food
254 resources (2) subdominants that aggressively defend or try to take over food resources and (3)
255 subordinates that defend only their nest. However, most ant assemblage lack of species from
256 the dominant category and some subdominant species clearly act as dominant (Cerdá *et al.*
257 2013). This pattern has been observed for *L. emarginatus* in the habitats of Crimea Mountains
258 where its colonies were the largest (around 30 000 workers, Stukalyuk and Radchenko 2011)
259 and dominated other species such as *C. piceus*. In our case, dominant and almost strict liquid
260 feeding species such as *L. emarginatus* (Blatrix *et al.* 2013) could strongly compete for the food
261 resources produced by the plants (directly such as nectar or indirectly such as aphids honeydew)
262 and outcompete less dominant and more diet generalist species such as *C. piceus* (Blatrix *et al.*
263 2013).

264

265

266 **3. Segregate and nested responses to latitude at different taxonomic levels**

267 Overall, floricolous ants showed a quadratic response to latitude, with maximum occurrence at
268 intermediate latitudes (around 45-46° N). Such pattern echoed the one previously described on
269 the species richness of coprophageous beetles studied along the same latitudinal range (Lobo *et*
270 *al.* 2002). According to Lobo *et al.* (2002), this pattern could be explained by maximum annual
271 and mean annual temperatures which are the most influential spatially structured climate
272 variables along latitudinal gradient of continental France.

273 We highlighted that the presence of the three main subfamilies of floricolous ants exhibited
274 different latitudinal optimums, with Myrmicinae and Dolichoderinae being restricted to lower
275 latitudes whereas Formicinae were more present at medium and high latitudes. Strikingly such
276 a segregated response of ant to latitude was also observed for the lower taxonomical levels we
277 studied, with the presence of the 3 genera of Formicinae showing segregated optimum along
278 the latitudinal gradient (from south to north France: *Camponotus*, *Serviformica* and *Lasius*) and
279 the two species of *Camponotus* showing the same pattern (from south to north: *C. lateralis* and
280 *C. piceus*). Such pattern could result from niche partitioning among ant taxa to minimise
281 competition for resources (reviewed by Schoener 1974), a phenomenon that has been shown to
282 be related to the distribution of ants along large scale environmental gradient (Machac *et al.*
283 2011). However, we also observed that the latitudinal segregation was taxonomically
284 aggregated which could be the sign of shared ancestral ecological characteristics. However,
285 more data on various ant species are needed to properly test for a phylogenetic signal in the
286 latitudinal optimum of ants.

287 **4. Heterogeneous responses to Urbanization and interaction with latitudinal** 288 **gradient**

289 Most ant taxa analysed here showed a negative response to urbanization gradient. This is in
290 accordance with previous studies highlighting a negative impact of urbanization on ant

291 abundance (Buczowski and Richmond 2012) or richness (McKinney 2008, Vepsäläinen *et al.*
292 2008). Such a negative effect has also been found for other floricolous arthropods, such as
293 Lepidopterans, Coleopterans and Dipterans (Deguines *et al.* 2012), but also for ground beetles
294 (Vergnes *et al.* 2014), suggesting that the effect of urbanization on arthropods is general.
295 However, the lower presence of ant visiting flowers in urbanized areas could also be link to a
296 decrease in the “attractivity” of flowers as resources. Urbanization strongly modifies the
297 environment (i.e. soil and air properties, carbon cycle and management) (McDonnell and Hahs
298 2008). These modifications could have altered the properties of nectar (attractiveness, quality
299 or quantity) (Clark *et al.* 2007, Meindl and Ashman 2013). Moreover, cities are highly
300 heterotrophic systems that produces a lot of resources for invertebrates (McIntyre 2000) such
301 as wastes that are known to be highly attractive for ants (Youngsteadt *et al.* 2014). Ant might
302 thus neglect floral resources in urban environment, to the profit of other urban specific
303 resources. Finally, exclusive competition by strict liquid eating and dominant ants such as *L.*
304 *emarginatus* could reinforce such a switch in food resource for omnivorous and less dominant
305 species such as *C. piceus* or *C. lateralis* (Blatrix *et al.* 2013, Cerdá *et al.* 2013).

306 As expected, we observed a contrasted response to urbanization along the latitudinal gradient
307 with a tendency for a stronger negative effect at lower latitudes. The increase in temperature
308 and decrease of soil moisture along urbanization gradient are considered as general trends
309 (McDonnell and Hahs 2008). However, in regions with a Mediterranean climate such as the
310 lowest latitudinal parts of France, an increase of soil moisture and a decrease of soil temperature
311 along urbanization gradient is frequently observed, mainly due to run-off on impervious
312 surfaces (Holway and Suarez 2006). Those colder and moister conditions are less favorable to
313 most ants, as observed at large scale across Europe (Kumschick *et al.* 2009).

314
315
316

317 **Conclusion**

318 Our analysis highlights that both latitude and urbanization affect the distribution of ant-flower
319 interactions and that the coupling of a large dataset collected by citizen scientists with
320 appropriate data validation by experts is an efficient and promising approach. Our results
321 suggested a strong impact of both evolutionary history and competition in shaping the
322 distribution of ant plant interaction across France.

323

324 **Declarations**

325 We wish to thank the hundreds of participants of the Spipoll program who collected the data
326 and Mathieu de Flores (OPIE) for coordinating this program.

327

328 **Conflict of interest disclosure**

329 The authors of this article declare that they have no financial conflict of interest with
330 the content of this article.

331

332 **Supporting information**

333 Additional Supporting Information may be found in the online version of this article:

334 **S1 Table.** Details of taxonomic levels between studied groups.

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