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1 **Feeding behaviour of red fox and domestic cat populations in suburban areas in**  
2 **the south of Paris**

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18 **Abstract (150-250 words)**

19 Among medium-sized carnivores, red foxes (*Vulpes vulpes*) and domestic cats (*Felis*  
20 *silvestris catus*) are the most abundant species in human-dominated landscapes  
21 worldwide. Both are known to be generalist predators that exploit a wide range of  
22 prey groups (e.g., mammals, birds, and invertebrates). Identifying red fox and  
23 domestic cat predation pressure on shared prey could shed light on their ecological  
24 role in shaping wildlife communities in human-dominated landscapes.

25 Here, we assess the seasonal diet of red foxes and domestic cats in terms of  
26 composition, breadth, and overlap. Over two years, we collected their scats across  
27 three human-dominated study sites: park ( $n = 220$  for foxes and  $n = 0$  for cats),  
28 agricultural land ( $n = 159$  for foxes and  $n = 146$  for cats), and managed forest ( $n =$   
29  $169$  for foxes and  $n = 47$  for cats). We detected similar diet breadth (B) for red foxes  
30 and domestic cats (B = 0.32 and B = 0.36, respectively) as well as strong dietary  
31 overlap (O = 0.83) between them. Moreover, the diet composition of both predators  
32 varied according to the study sites and seasons. Our results confirm the highly  
33 flexible trophic behaviour of these carnivores at the study sites, probably as a  
34 consequence of prey availability, and also the simultaneity of their predation over  
35 the same prey groups. Future studies should simultaneously monitor predator diet as  
36 well as predator and prey abundance in human-dominated landscapes to better  
37 understand the predatory impact of red foxes and domestic cats.

38 **Keywords**

39 Diet breadth; diet overlap; domestic cat; red fox; human-dominated landscapes

## 40 **Introduction**

41 By 2050, more than half of the world's population will live in urbanized areas (United  
42 Nations 2019). Consequently, understanding the functioning of these ecosystems is  
43 necessary in order to preserve both biodiversity and human life quality. Human-  
44 dominated landscapes share a set of general biotic and abiotic characteristics such as the  
45 alteration of species richness (McKinney 2008), the variation of microclimatic  
46 conditions (Santamouris et al. 2001), the availability of new resources such as  
47 anthropogenic food refuse (Fleming and Bateman 2018), and the lack or reduced  
48 number of large carnivores (Crooks 2002; Iossa et al. 2010; Bateman and Fleming  
49 2012). In this context, medium-sized carnivores may be “released” in the absence of  
50 top-predators (Crooks and Soulé 1999), thus influencing prey populations through top-  
51 down processes, as already demonstrated at continental (Ripple et al. 2013) and local  
52 scales (Jiménez et al. 2019).

53 Among medium-sized carnivores, the red fox (*Vulpes vulpes*) is one of the most  
54 widespread species (Schipper et al. 2008), while the domestic cat (*Felis silvestris catus*)  
55 is one of the most popular pets worldwide. Out of 18.83 million pets in France, 11.4  
56 million are cats. Moreover, the generalist trophic behaviour of red foxes and domestic  
57 cats makes them successful species in human-dominated landscapes (Bateman and  
58 Fleming 2012). Red fox diets in urban areas are mostly characterized by the presence of  
59 anthropogenic food refuse (Harris 1981; Doncaster et al. 1990; Contesse et al. 2004;  
60 Hegglin et al. 2007; Meckstroth et al. 2007), while in rural areas, they are more  
61 diversified with mammals and birds (Goldyn et al. 2003), mammals, invertebrates, and  
62 fruits (Ghoshal et al. 2016), or invertebrates and fruits (Dell'Arte et al. 2005) as the  
63 principal food categories. Like red foxes, domestic cats living in urban areas consume  
64 not only anthropogenic refuse (Eberhard 1954; Jackson 1951) but also mammals and

65 birds (Gordon et al. 2010; Tschanz et al. 2011; Thomas et al. 2012). In rural areas,  
66 mammals and birds are among the principal prey categories in domestic cat diet (Kays  
67 and Dewan 2004; Brickner-Braun et al. 2007; Flux 2007; Morgan et al. 2009; van  
68 Heezik et al. 2010). Little is known, however, about how these predators interact with  
69 each other or with their shared prey in human-dominated landscapes. In natural or semi-  
70 natural habitats, several studies have assessed the influence of fox presence on cat  
71 trophic behaviour (Molsher et al. 2017). Moreover, in other natural habitats there exist  
72 some degree of trophic competition between these two predators (Catling 1988; Risbey  
73 et al. 1999; Glen et al. 2011)

74 Simultaneous monitoring of red fox and domestic cat diets is needed in order to  
75 determine their degree of trophic overlap, better assess their concomitant potential  
76 predation pressure, and clarify their trophic role in shaping prey communities. To date,  
77 however, only one study (Meckstroth et al. 2007) has carried out the simultaneous  
78 monitoring of red fox and domestic cat diets in a human-dominated landscape, but none  
79 has investigated their degree of diet overlap. In the present study, we firstly aimed to  
80 describe red fox and domestic cat diets in three human-dominated landscapes (urban  
81 park, agricultural land, and managed forest) across seasons and then estimate their diet  
82 breadth and overlap. We hypothesised that both predators consumed a wide range of  
83 prey (e.g., large diet breadth) and shared most of them (e.g., high degree of diet  
84 overlap), will confirm their generalist trophic behaviour mainly driven by temporal and  
85 local specificities.

86

## 87 **Materials and methods**

### 88 *Study sites*

89 Red fox and domestic cat populations were non-invasively monitored by collecting  
90 faecal samples (hereafter, scats) at three suburban study sites (Fig. 1). Sceaux urban  
91 park (hereafter, park) (48°46'03.17''N, 2°17'47.48''E), located 20 km south of Paris,  
92 covers an area of 1.81 km<sup>2</sup> and comprises three main habitat types: open areas (lawns  
93 and meadows), wooded areas (composed of 16% *Fraxinus* sp., 14% *Acer platanoides*,  
94 12% *Acer pseudoplatanus*, and 9% *Carpinus*), and French formal gardens  
95 (predominately ornamental species) (Hauts-de-Seine Conseil Général 2015). The  
96 agricultural area of Saclay (hereafter, agricultural land) (48°42'32.18''N,  
97 2°10'33.00''E) is located between the north of the Essonne department and the  
98 southeast of the Yvelines department. This fertile agricultural land extending over 27  
99 km<sup>2</sup> has a long agricultural tradition with the primary crops of colza, wheat, and barley.  
100 Currently, this area is facing urbanisation pressure due to the development of a  
101 university and laboratory cluster (Spaak 2013). Rambouillet forest (hereafter, forest)  
102 (48°40'29.84''N, 1°48'27.17''E), located in the south of the Yvelines department, is  
103 one of the largest forests in the Île-de-France region. This wooded area of 200 km<sup>2</sup>,  
104 mainly composed of oaks and coniferous (68% and 25%, respectively), covers a  
105 territory of 29 municipalities (Ministère de l'agriculture et de la pêche 2015).

#### 106 *Sampling protocol*

107 One month prior to the start of predator scat sampling, all study sites were cleaned by  
108 removing old scats. Scat sampling was carried out four times per year in the middle of  
109 each season (October/autumn; January/winter; April/spring; July/summer) over two  
110 consecutive years (2014-2016) for each of the three study sites. Carnivora scats are  
111 cylindrical (i.e., sausage-shaped) with sub-division tapped at one of the extremities  
112 (Chame 2003). These characteristics may therefore promote scat misidentifications  
113 among mammalian carnivores of similar body size (Reid 2015; Morin et al. 2016). Red

114 fox and domestic cat scats, however, can be differentiated by their morphometry (Bang  
115 and Dahlström 1975) and secondarily by their place of deposition, dietary content, and  
116 odour. Red fox scats (8-10 cm length and 2 cm width) are larger than those of domestic  
117 cats (6-8 cm length and 1-1.5 cm width) (Chame 2003). Moreover, red fox scats are  
118 tubular, long, and twisted with pointed ends, whereas domestic cat scats are smoothed  
119 and compacted with well-defined segments and only one tapered extremity (Chame  
120 2003). Red foxes usually deposit scats in prominent positions along tracks to signal  
121 their presence to other individuals, whereas domestic cats tend to bury theirs (Seton  
122 1925, Gibbons 2008). Regarding dietary contents, domestic cat scats strictly reflect their  
123 carnivorous diet with the additional presence of grass leaves ingested to aid hair  
124 elimination and/or Gramineae seeds indirectly ingested with the grass leaves (Chame  
125 2003). Fresh red fox scats present a strong “foxy” smell like middle skunk (Gibbons  
126 2008). Scats were collected by walking along the same paths in each study site and  
127 season. They were individually geolocalised, stored in separate plastic bags, and frozen  
128 (- 20°C) until analysis. In this study, we aimed to detect the heterogeneity of predator  
129 diet in the main suburban habitats and across seasons. Thus, though informative, within-  
130 habitat site replications were not assessed; indeed, this was not possible in the park and  
131 agricultural land due to their limited areas. Because of the low number of domestic cat  
132 scats collected in the forest and park, we asked volunteer owners to collect the scats of  
133 their own vagrant cats during each study period. Four owners from each study site  
134 (forest and park) with one to three cats in their house collaborated with us.  
135 Due to the small number of red fox and domestic cat scats containing prey remains in  
136 some seasons and years, we decided to pool samples by season (i.e., without  
137 considering the year). Only seasons with at least 10 scats with prey remains per predator  
138 species were included in the following analyses (Table S1). Despite the collaboration of

139 cat owners, many of the collected scats did not contain any prey remains. As a result,  
140 we did not have sufficient numbers of cat scats from the park for all seasons or from the  
141 forest in spring to include them in the analyses (Table S1).

#### 142 *Laboratory analyses*

143 Scats were analysed macroscopically and microscopically. Macroscopic analysis was  
144 performed by washing the scats individually under a stream of water in a 2 µm sieve.  
145 We excluded scats without prey remains (i.e., feathers, hairs, bones, seeds). Prey  
146 remains were identified under a binocular to the finest taxonomic level possible using  
147 the bone reference collections from the National Museum of Natural History in Paris for  
148 mammals and birds, and identification keys for invertebrates and fruits before validating  
149 our identifications with specialists of the targeted groups. Indigestible prey remains  
150 (e.g., hair, teeth, bones, skin, scales, feathers, exoskeletons, seeds from fleshy fruits)  
151 were then classified into 16 main food categories for a more accurate diet comparison:  
152 Microtidae (including *Myodes glareolus*, *Microtus agrestis*, and *Microtus arvalis*),  
153 Muridae (including *Apodemus sylvaticus*, *Mus musculus*, *Rattus* sp., *Rattus norvegicus*,  
154 and *Rattus rattus*), Soricidae (including *Sorex coronatus*, *Crocidura leucodon*, and  
155 *Crocidura russula*), Leporidae (including *Oryctolagus cuniculus* and *Lepus europaeus*),  
156 small birds (~ size of Passeroidea), large-medium birds (~ size of Corvoidea),  
157 Coleoptera, Hymenoptera, Dermaptera, Orthoptera, Heteroptera, Lepidoptera,  
158 Arachnida, earthworms, small fruits (*Prunus cerasus*, *P. prunus*, and *Rubus ulmifolius*),  
159 and large fruits (*Malus* sp. and *Pyrus* sp.). We also reported the frequency of nonorganic  
160 (e.g., plastic, foil paper) anthropogenic refuse (hereafter, refuse). Coprophagous,  
161 recycling, and ticks were excluded from the invertebrate prey.



162 Microscopic analysis was carried out by subsampling ~ 2.5 mg of each homogenised  
163 predator scat on microscope slides to quantify earthworm consumption based on chaetae  
164 counts (Reynolds and Aebischer 1991).

165 *Data analyses*

166 For each scat, we firstly determined the minimum number of consumed prey individuals  
167 in each scat ( $prey_{MNI}$ ) for the main food categories (i.e., excluding refuse). For birds,  
168 mammals, and terrestrial arthropods, we counted the number of identical prey fragments  
169 contained in each predator scat. For fleshy fruits,  $prey_{MNI}$  per predator scat was  
170 calculated based on the mean number of seeds (MNS) per fruit collected at the study  
171 sites: *Rubus ulmifolius* (n=150, MNS = 52.64); *Prunus prunus* (n=39, MNS = 1); *P.*  
172 *cerasus* (n=30, MNS = 1), *Malus* sp. (n=73, MNS = 4.49), and *Pyrus* sp. (n=71, MNS =  
173 4.72). For earthworms, we collected the most abundant species (*Aporrectodea*  
174 *caliginosa*, *A. giardi*, *Allolobophora icterica*, and *Octolasion cyaneum*) from our study  
175 sites to measure and calculate their mean fresh weights (g), length (cm), number of  
176 segments per individual, and number of chaetae per segment.  $prey_{MNI}$  for earthworms  
177 per scat was obtained as follows:

178 
$$(i) \text{ no. chaetae in scat} = \frac{\text{no. chaetae} \times \text{total scat weight (dry)}}{\text{weight of analysed sample (0.0025 gr)}}$$

179

180 
$$(ii) \text{ no. segments} = \frac{\text{no. chaetae in scat}}{\text{mean no. chaeta per segment}}$$

181

182 
$$(iii) \text{ prey}_{MNI} = \frac{\text{no. of segments}}{\text{no. of segments in one earthworm}}$$

183 To quantify the ingested prey biomass contained in each scat ( $prey_{IBS}$ ), we firstly  
184 calculated the total ingested biomass (TIB) by multiplying the  $prey_{MNI}$  of each prey by  
185 its mean mass (MM). The biomass of small mammals (MM= 57.32 g) and birds (MM=

186 302.54 g) was calculated using weight data extracted from the Amniote trait database  
187 (Myhrvold et al. 2015). We estimated invertebrate MM by weighing field-collected  
188 individuals from the orders most commonly consumed by the studied predators:  
189 Coleoptera (n=156, MM= 0.29 g), Hymenoptera (n=26, MM= 0.01 g), Dermaptera  
190 (n=20, MM= 0.03 g), Orthoptera (n=71, MM= 0.10 g), Heteroptera (n=76, MM= 0.02  
191 g), and Lepidoptera (n=92, MM= 0.02 g), as well as the class Arachnida (n=87, MM=  
192 0.01 g). Fruit MM was obtained by collecting and weighing the following fruits from  
193 the study sites: *Rubus ulmifolius* (n=150, MM= 2.19 g), *Prunus prunus* (n=39, MM=  
194 15.09 g), *P. cerasus* (n=30, MM= 3.70 g), *Malus* sp. (n=73, mean MM= 90.01 g), and  
195 *Pyrus* sp. (n=71, MM= 98.55 g). Since red foxes and domestic cats are known to ingest  
196 large body mass prey (e.g., Leporidae, large birds) only partially (Artois 1989; Bonnaud  
197 et al. 2007), we estimated the ingested proportion of lagomorphs and large-medium  
198 birds by calculating the maximum food intake per scat of each predator. To do so, we  
199 selected red fox (n=75) and domestic cat (n=53) scats containing only small mammals  
200 (i.e., prey entirely ingested) and multiplied their  $prey_{MNI}$  by their MM to obtain a  
201 maximum ingested biomass (MIB in g of fresh biomass) for each predator scat. MIB  
202 was 244.09 g and 232.40 g for red fox and domestic cat, respectively. We then  
203 calculated the ingested biomass of each prey category per scat ( $prey_{IBS}$ ) by using one of  
204 the two following formulas. If the TIB did not exceed the MIB, we applied the formula:

205

$$206 \quad (iv) \text{ prey}_{IBS} = \text{small prey}_i \text{ MM} \times \text{small prey}_i \text{ MNI}$$

207

208 If the TIB exceeded the MIB due to the consumption of large prey<sub>j</sub> like lagomorph and  
209 large-medium birds, for instance, we applied the following formula:

210

211 
$$(v) \text{prey}_{IBS} = \frac{MIB - \sum_i^n (\text{small prey}_i \text{ MM} \times \text{small prey}_i \text{ MNI})}{RIB_j}$$

212  
213 Where  $RIB_j$  is the relative ingested biomass of each large prey calculated as follows:

214

215 
$$(vi) RIB_j = \frac{(\text{large prey}_j \text{ biomass} \times \text{large prey}_j \text{ number})}{\sum_1^n (\text{large prey}_j \text{ biomass} \times \text{large prey}_j \text{ number})}$$

216

217 *Effects of study sites and seasons on predator diet*

218 We chose multivariate generalised linear models (hereafter, GLMs) to detect factors  
219 (i.e., predator, study site, and season) that could affect diet composition, because our  
220 dietary data had a strong mean-variance relationship that was taken into account in these  
221 models (Wang et al. 2016). Firstly, we fitted one global GLM using the following  
222 formula:  $\text{diet} \sim \text{predator} + \text{study site} * \text{season}$ . Secondly, we fitted one GLM for each  
223 predator species using the following formula:  $\text{predator diet} \sim \text{study site} * \text{season}$ . We  
224 then ran univariate analysis of variance for each prey category and adjusted the p-value  
225 for multiple testing with a step-down resampling procedure (Wang et al. 2016). We  
226 used 999 bootstrap iterations to sample multivariate GLM residuals. Models were fitted  
227 with the *manyglm* function from the *mvabund* package (Wang et al. 2016). Although we  
228 only discuss the results from the models with  $\text{prey}_{IBS}$  as the response variable, as it is  
229 the best approximation of the true diet of predators (Klare et al. 2011), we also included  
230 the results from the global model for each of the two diet descriptors ( $\text{prey}_{MNI}$  and  
231  $\text{prey}_{MNI}$ ) as response variables (Table S2) and from the model using  $\text{prey}_{MNI}$  as the  
232 response variable (Table S3).

233 *Predator diet breadths and overlaps*

234 We used  $\text{prey}_{\text{MNI}}$  to calculate the degree of trophic specialisation for each studied  
235 predator by estimating their diet breadth (B) and degree of diet overlap (O) using the  
236 *nichevar* and *nicheoverlap* functions from the *indicspecies* package, respectively  
237 (Caceres and Legendre 2009). Diet breadth ranges from 0 to 1, with values close to 0 for  
238 specialised populations and values close to 1 for generalists. Diet overlap ranges from 0  
239 to 1, with values close to 0 for low diet overlap between predator populations and  
240 values close to 1 for high diet overlap.

241 We visually assessed dietary overlap between predators, study sites, and seasons using  
242 nonmetric multidimensional scaling (NMDS) plots. This multivariate method is based  
243 on a triangular resemblance matrix of Bray-Curtis similarities among all pairs of  
244 samples. We used the *metaMDS* function from the *vegan* package (Oksanen et al. 2018)  
245 to produce NMDS plots. All statistical analyses were carried out using R Studio version  
246 1.1.463. (R Core Team 2019).

247

## 248 **Results**

249 In total, we collected 1,073 scats, but 332 did not contain any wild prey remains (i.e.,  
250 only highly digestible organic matter like industrial food and/or refuse), with 55% of  
251 them belonging to red foxes (park:  $n = 94$ , agricultural land:  $n = 24$ , managed forest:  $n =$   
252  $65$ ) and 45% to domestic cats (park:  $n = 85$ , agricultural land:  $n = 21$ , managed forest:  $n =$   
253  $43$ ) (Table S1). From the remaining 741 scats containing prey remains, 74% belonged  
254 to red foxes (park:  $n = 220$ , agricultural land:  $n = 159$ , managed forest:  $n = 169$ ) and  
255 26% to domestic cats (park:  $n = 0$ , agricultural land:  $n = 146$ , managed forest:  $n = 47$ )  
256 (Table S1). Out of these 741 scats, 41 scats contained prey remains that were not  
257 attributable to the 16 main prey groups defined above (e.g., scats containing  
258 unidentifiable parts of invertebrates, seeds, feathers, or hairs). This resulted in the

259 inclusion of 700 scats in prey<sub>IBS</sub> and prey<sub>MNI</sub> models, corresponding to 699 degrees of  
260 freedom in general models and 521 and 177 degrees of freedom in red fox ( $n = 522$ ) and  
261 domestic cat ( $n = 178$ ) models, respectively.

262 We identified a total of 6,742 prey items. Based on prey<sub>IBS</sub>, red fox diet was mainly  
263 composed of Rodentia (37%) and large-medium birds (28%), and domestic cat diet of  
264 Leporidae (41%) and large-medium birds (27%) (Table 1). Based on the prey<sub>MNI</sub>, red  
265 fox diet was mainly composed of earthworms (53%), and domestic cat diet of  
266 earthworms (40%) and Microtidae (21%) (Table 1).

267 The composition of both predators' diets (prey<sub>IBS</sub>) was influenced by predator species,  
268 study sites, seasons, and the interaction between study sites and seasons (Table S2a).

269 Predator species affected diet prey<sub>IBS</sub> in terms of Leporidae, Microtidae, Coleoptera,  
270 earthworms, and small fruits. Study site affected both predators' consumption of  
271 Leporidae, Microtidae, Muridae, Soricidae, large-medium birds, Coleoptera, and  
272 earthworms. Seasons influenced both predators' diets in terms of Coleoptera,  
273 earthworms, and small fruits. The interaction between study site and season also  
274 affected both predators' diets in terms of Leporidae, large-medium birds, Coleoptera,  
275 and small fruits (Table S2a).

#### 276 *Red fox diet*

277 The composition of red fox diet (prey<sub>IBS</sub>) was influenced by study sites, seasons, and the  
278 interaction between study sites and seasons (Table 2a). Study site affected red fox  
279 prey<sub>IBS</sub> in terms of Microtidae, Muridae, large-medium birds, Coleoptera, earthworms,  
280 and small fruits. Seasons influenced red fox consumption of Coleoptera, earthworms,  
281 and small fruits. The interaction between study site and season also affected red fox  
282 prey<sub>IBS</sub> in terms of large-medium birds, Coleoptera, and small fruits (Table 2a).

283 Based on the ingested prey biomass ( $\text{prey}_{\text{IBS}}$ ), in the park, red fox diet was mainly  
284 composed of large-medium birds (66%), especially in autumn (73%), spring, (99%),  
285 and summer (60%) (Table 1). In agricultural land, red fox diet principally comprised  
286 large-medium birds (35%), especially in autumn (50%) and summer (37%), followed by  
287 Leporidae (28%), mainly in autumn (37%), winter (20%), and summer (30%) (Table 1).  
288 In the forest, red fox diet was mainly composed of Leporidae (36%), especially in  
289 autumn (98%) and spring (98%), followed by Muridae (29%), principally in winter  
290 (53%) (Table 1).

291 Based on the minimum number of ingested individuals ( $\text{prey}_{\text{MNI}}$ ), in the park, red fox  
292 diet was mainly composed of earthworms (61%), particularly in autumn (90%), winter  
293 (77%), and spring (87%). In agricultural land, red fox diet principally comprised small  
294 fruits (38%), especially in summer (55%), followed by earthworms (33%), mostly in  
295 autumn (61%), winter (36%), and spring (64%). In the forest, earthworms were the  
296 principal food category in red fox diets (56%), especially in winter (79%) and spring  
297 (64%) (Table 1).

#### 298 *Domestic cat diet*

299 Domestic cat diet composition was influenced by the seasons as well as the interaction  
300 between study site and season. In particular, seasons had an influence on domestic cat  
301  $\text{prey}_{\text{IBS}}$  in terms of earthworm biomass (Table 2b).

302 Based on the ingested prey biomass ( $\text{prey}_{\text{IBS}}$ ), in agricultural land, domestic cat diet was  
303 mainly composed of Leporidae (57%), especially in autumn (67%), winter (52%), and  
304 spring (77%) (Table 1). In the forest, domestic cat diet principally comprised Muridae  
305 (43%), particularly in summer (70%), followed by large-medium birds (18%),  
306 especially in summer (64%) (Table 1).

307 Based on the minimum number of ingested individuals ( $prey_{MNI}$ ), in agricultural land,  
308 domestic cat diet was mainly composed of earthworms (48%), particularly in autumn  
309 (60%), winter (64%), and spring (34%), followed by Microtidae (20%), especially in  
310 summer (34%) (Table 1). In the forest, domestic cat diet mainly comprised earthworms  
311 (22%), particularly in autumn (65%) and winter (47%), followed by Microtidae (22%),  
312 especially in summer (52%) (Table 1).

### 313 *Diet breadth and overlap*

314 According to the results of the diet breadth index, both predators exhibited a narrow diet  
315 breadth at all study sites and across seasons ( $B < 0.40$ ), with the diet breadth of each  
316 predator being similar (red fox:  $B = 0.32$ , 95% CI [0.29, 0.34]; domestic cat:  $B = 0.36$ ,  
317 95% CI [0.31, 0.39]) across study sites and seasons (Fig. 2).

318 Interestingly, in agricultural land, we found a high degree of diet overlap between red  
319 fox and domestic cat populations across all seasons ( $O > 0.75$ ) except summer ( $O =$   
320  $0.33$ , 95% CI [0.20, 0.56]) (Table S4). During this season, dissimilarity between red fox  
321 and domestic cat diet (i.e., points located far from each other with little or no overlap)  
322 was higher compared to the other seasons (Fig. 3a). By contrast, we detected higher  
323 variations in the diet overlap between red fox and domestic cat populations in the forest  
324 compared to agricultural land, with the highest value found in winter ( $O = 0.92$  95% CI  
325 [0.05, 0.99]) and the lowest in summer ( $O = 0.25$  95% CI [0.04, 0.60]) (Table S4). In  
326 winter, red fox and domestic cat diet showed the highest similarity (i.e., most points are  
327 spatially close to each other or overlapping), while the lowest diet similarity was  
328 observed in summer (Fig. 3b). Due to the limited number of collected cat scats in some  
329 habitats and seasons, we did not calculate the diet overlap between red fox and domestic  
330 cat populations in the forest in spring or in the park for all seasons.

331

332 **Discussion**

333 Results obtained in this study were only based on the analysis of scats containing wild  
334 prey remains (i.e., 75% and 56% of red fox and domestic cat scats, respectively). The  
335 high proportion of domestic cat scats without any wild prey remains (i.e., containing  
336 only highly digestible organic matter like industrial food and/or refuse) is partly due to  
337 the high percentage (70%) of scats that were provided by cat owners, meaning that  
338 domestic cats were primarily sustained by human-mediated food while having the  
339 opportunity to wander and feed on wild prey. Even if the percentage of red fox scats  
340 containing only refuse and/or industrial food is lower than that of domestic cat scats,  
341 this indicates that red foxes, particularly in suburban areas, are able to feed on human-  
342 mediated food. This feeding habit may provide them with some adaptive and/or survival  
343 advantages.

344 *Red fox and domestic cat diets*

345 The trophic index based on ingested prey biomass ( $\text{prey}_{\text{IBS}}$ ) revealed that large-medium  
346 birds and mammals were the prey categories most contributing to red fox and domestic  
347 cat food bolus. Invariably, red fox and domestic cat diets were dominated by large prey  
348 (i.e., large-medium birds and Leporidae) and/or medium-sized prey (Muridae) across all  
349 study sites and seasons. This result suggests that the survival of both predators mainly  
350 depends on prey with a large biomass (e.g., medium-large birds, Leporidae), probably  
351 because one killed individual represents a large source of metabolizable energy.

352 The trophic index based on the minimum number of ingested individuals ( $\text{prey}_{\text{MNI}}$ )  
353 revealed that earthworms were the most abundantly consumed prey in red fox diet. This  
354 result is in good agreement with other studies once refuse is removed from red fox diet  
355 (MacDonald 1980; Harris 1981; Doncaster et al. 1990; Reynolds and Aebischer 1991;  
356 Saunders et al. 1993; Soulsbury et al. 2008). In domestic cat diet, earthworms along



357 with Microtidae were the most abundantly consumed prey. While the presence of  
358 chaetae in predator scats may be increased by phenomena such as soil contamination  
359 and secondary predation (i.e., chaetae would have persisted after two digestions),  
360 potentially leading to a slight overestimation of earthworm consumption, the high  
361 number of consumed earthworms stresses the importance of this prey type for both red  
362 foxes and domestic cats, as it may supply these predators with their protein  
363 requirements within human-dominated landscapes. Even if striking, the consumption of  
364 earthworms (protein-rich prey) by domestic cats is probably opportunistic and focussed  
365 on anecic and/or epigeic earthworms (Lee 1985), which are readily available and easy to  
366 catch in agricultural and forest soils. This interesting result should be confirmed (i.e.,  
367 earthworm species identification) in future studies using metabarcoding approaches, for  
368 example (Bienert et al. 2012; Boyer et al. 2013; Pansu et al. 2015). In general, the  
369 macro- and microscopic diet analyses of predator diets would benefit from  
370 metabarcoding approaches to verify prey identification, detect and identify digested  
371 soft-bodied prey (e.g., insect larvae, egg content), and confirm predator scat  
372 identification (Pompanon et al. 2012; Galan et al. 2018).

### 373 *Specific spatiotemporal diet patterns for red foxes and domestic cats*

374 Red fox populations showed study site specificities in terms of the proportion of  
375 ingested biomass for certain prey categories (Microtidae, Muridae, large-medium birds,  
376 Coleoptera, earthworms, and small fruits) as well as seasonal dietary shifts for some of  
377 these resources (Coleoptera, earthworms, and small fruits) (Tables 1 and 2a).  
378 These results are in good agreement with and support the generalist and opportunistic  
379 trophic behaviour of red foxes (Sillero et al. 2004). Thanks to this trophic behaviour, red  
380 foxes could adapt their diet in contrasting human-dominated landscapes according to the

381 abundance and availability of associated prey communities and fruit resources (e.g.,  
382 emergence of Coleoptera, fructification of fleshy fruits) (Díaz-Ruiz et al. 2013).

383 In contrast to red fox diet, domestic cat diet (in terms of ingested prey biomass) was  
384 relatively homogeneous across study sites and mainly focussed on mammals (Leporidae  
385 and Muridae; Gillies and Fitzgerald 2005 (New Zealand); Kays and Dewan 2004 (US);  
386 Krauze-Gryz et al. 2012 (Europe)) and secondarily on large-medium birds, with only  
387 the proportion of ingested earthworm biomass changing seasonally (Tables 1 and 2b).

388 This suggests that cats are highly adaptable and efficient hunters, which allows them to  
389 survive and reproduce without regard to the type of habitat, thus confirming the  
390 opportunistic but strictly carnivore trophic behaviour of domestic cats (Bradshaw et al.  
391 1996; Medina et al. 2011). By consequence, the increased number of vagrant domestic  
392 cats due to the higher human population density can lead to negative effects on bird,  
393 mammal, and reptile population dynamics in many different types of habitats (Woods et  
394 al. 2003; Dauphiné and Cooper 2009; Blancher 2013; Loss et al. 2013; Doherty et al.  
395 2015). As the opportunistic behaviour of these predators likely depends on resource  
396 abundance and availability, which are rarely monitored and quantified, this should be  
397 investigated in future studies to detect potential patterns of prey preferences.

398 At all the study sites, both red foxes and domestic cats abundantly consumed  
399 earthworms (in prey<sub>MNI</sub>) in autumn, winter, and spring, probably due to the scarcity of  
400 other prey categories during these seasons of relatively low productivity. The use of this  
401 alternative high-protein prey may allow red foxes and domestic cats to maintain stable  
402 populations all year round within degraded human-dominated landscapes. Interestingly,  
403 in agricultural land, domestic cats turned to the consumption of *Microtus agrestis*  
404 individuals as observed in other rural areas in Europe (Krauze-Gryz et al. 2012), while  
405 red foxes shifted their diet to temporarily abundant small fruits that are rich in

406 carbohydrates, minerals, and vitamins (e.g., *Prunus cerasus*, *P. prunus*, *Rubus*  
407 *ulmifolius*) (Table 1). Red fox consumption of fruits has already been described in other  
408 studies in Europe (Contesse et al. 2004) and Asia (Dell'Arte et al. 2005; Ghoshal et al.  
409 2016). In addition to being an alternative source of nutrient for foxes, these fruits  
410 contained seeds that can be efficiently dispersed (Herrera 1989; Matías et al. 2010),  
411 leading to the conservation of the vegetation structure of these habitats. Last but not  
412 least, the consumption of voles by domestic cats in summer likely corresponds to a peak  
413 abundance of this prey, which supports the opportunistic trophic behaviour of cats. As  
414 domestic cats are one of the major predators of voles (Lin and Batzli 1995), they could  
415 modify the cyclicity of the prey population dynamics (Hansson 1988) and indirectly  
416 affect the trophic behaviour of other predators sharing this prey such as red foxes.

#### 417 *Diet breadth and overlap*

418 Although we showed that red foxes and domestic cats are able to exploit a wide  
419 spectrum of trophic resources (i.e., mammals, birds, invertebrates, and fruits) within  
420 human-dominated landscapes, these predators exhibit quite a narrow diet breadth  
421 similarly to those described by other authors in natural habitats (Drygala et al. 2014;  
422 Vlasseva et al. 2017; Széles et al. 2018). This result confirms that these predators hunt  
423 targeted prey groups with a focus on large birds and mammals.

424 Because foxes and cats had similarly varied diets across habitat types and seasons, we  
425 have confidence in the main result of a high dietary overlap despite the lack of within-  
426 habitat site replication.

427 These are the first results regarding the degree of diet overlap between red foxes and  
428 domestic cats within human-dominated landscapes, which are in good agreement with  
429 those found in natural habitats (Paltridge 2002; Woinarski et al. 2017). In our study, in  
430 summer, red fox and domestic cat diets only marginally overlapped, suggesting that they

431 can hunt a wider prey spectrum to reduce their degree of trophic overlap through niche  
432 partitioning. On the contrary, diet overlaps between red foxes and domestic cats were  
433 particularly high during the less productive seasons (i.e., autumn, winter, and spring)  
434 when they have to share scarcer main and alternative prey (i.e., mammals, birds, and  
435 earthworms). This indicates that competition between red foxes and domestic cats may  
436 occur, particularly if these predators are in high abundance in city centres (Šálek et al.  
437 2015; Flockhart et al. 2016) and probably more broadly in human-dominated areas.  
438 However, competition for food between species is eased by their generalist behaviour.  
439 In addition, these high seasonal diet overlaps between red foxes and domestic cats may  
440 exacerbate their predation pressure over shared prey populations and can lead to  
441 potential negative effects on shared prey population dynamics. To quantify predation  
442 impacts on prey population dynamics, future studies should simultaneously monitor  
443 predator diets as well as prey and predator availabilities through space and time.

444

#### 445 **Author's contributions**

446 IC collected and analysed the data and led the writing of the manuscript. DZL  
447 contributed to performing the diet descriptors. EB conceived the ideas and designed the  
448 methodology. All authors contributed to the writing and gave their final approval for  
449 publication.

450

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