



# Feeding behaviour of red fox and domestic cat populations in suburban areas in the south of Paris

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## Abstract

Among medium-sized carnivores, red foxes (*Vulpes vulpes*) and domestic cats (*Felis silvestris catus*) are the most abundant species in human-dominated landscapes worldwide. Both are known to be generalist predators that exploit a wide range of prey groups (e.g., mammals, birds, and invertebrates). Identifying red fox and domestic cat predation pressure on shared prey could shed light on their ecological role in shaping wildlife communities in human-dominated landscapes. Here, we assess the seasonal diet of red foxes and domestic cats in terms of composition, breadth, and overlap. Over two years, we collected their scats across three human-dominated study sites: park ( $n = 220$  for foxes and  $n = 0$  for cats), agricultural land ( $n = 159$  for foxes and  $n = 146$  for cats), and managed forest ( $n = 169$  for foxes and  $n = 47$  for cats). We detected similar diet breadth (B) for red foxes and domestic cats ( $B = 0.32$  and  $B = 0.36$ , respectively) as well as strong dietary overlap ( $O = 0.83$ ) between them. Moreover, the diet composition of both predators varied according to the study sites and seasons. Our results confirm the highly flexible trophic behaviour of these carnivores at the study sites, probably as a consequence of prey availability, and also the simultaneity of their predation over the same prey groups. Future studies should simultaneously monitor predator diet as well as predator and prey abundance in human-dominated landscapes to better understand the predatory impact of red foxes and domestic cats.

**Keywords** Diet breadth · Diet overlap · Domestic cat · Red fox · Human-dominated landscapes

## Introduction

By 2050, more than half of the world's population will live in urbanized areas (United Nations 2019). Consequently, understanding the functioning of these ecosystems is necessary in order to preserve both biodiversity and human life quality. Human-dominated landscapes share a set of general biotic

and abiotic characteristics such as the alteration of species richness (McKinney 2008), the variation of microclimatic conditions (Santamouris et al. 2001), the availability of new resources such as anthropogenic food refuse (Fleming and Bateman 2018), and the lack or reduced number of large carnivores (Crooks 2002; Iossa et al. 2010; Bateman and Fleming 2012). In this context, medium-sized carnivores may be “released” in the absence of top-predators (Crooks and Soulé 1999), thus influencing prey populations through top-down processes, as already demonstrated at continental (Ripple et al. 2013) and local scales (Jiménez et al. 2019).

Among medium-sized carnivores, the red fox (*Vulpes vulpes*) is one of the most widespread species (Schipper et al. 2008), while the domestic cat (*Felis silvestris catus*) is one of the most popular pets worldwide. Out of 18.83 million pets in France, 11.4 million are cats. Moreover, the generalist trophic behaviour of red foxes and domestic cats makes them successful species in human-dominated landscapes (Bateman and Fleming 2012). Red fox diets in urban areas are mostly characterized by the presence of anthropogenic food refuse (Harris 1981; Doncaster et al. 1990; Contesse et al. 2004; Hegglin et al. 2007; Meckstroth et al. 2007), while in rural areas, they are more diversified with mammals and birds

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(Goldyn et al. 2003), mammals, invertebrates, and fruits (Ghoshal et al. 2016), or invertebrates and fruits (Dell'Arte et al. 2005) as the principal food categories. Like red foxes, domestic cats living in urban areas consume not only anthropogenic refuse (Eberhard 1954; Jackson 1951) but also mammals and birds (Gordon et al. 2010; Tschanz et al. 2011; Thomas et al. 2012). In rural areas, mammals and birds are among the principal prey categories in domestic cat diet (Kays and Dewan 2004; Brickner-Braun et al. 2007; Flux 2007; Morgan et al. 2009; van Heezik et al. 2010). Little is known, however, about how these predators interact with each other or with their shared prey in human-dominated landscapes. In natural or semi-natural habitats, several studies have assessed the influence of fox presence on cat trophic behaviour (Molsher et al. 2017). Moreover, in other natural habitats there exist some degree of trophic competition between these two predators (Catling 1988; Risbey et al. 1999; Glen et al. 2011).

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

## Materials and methods

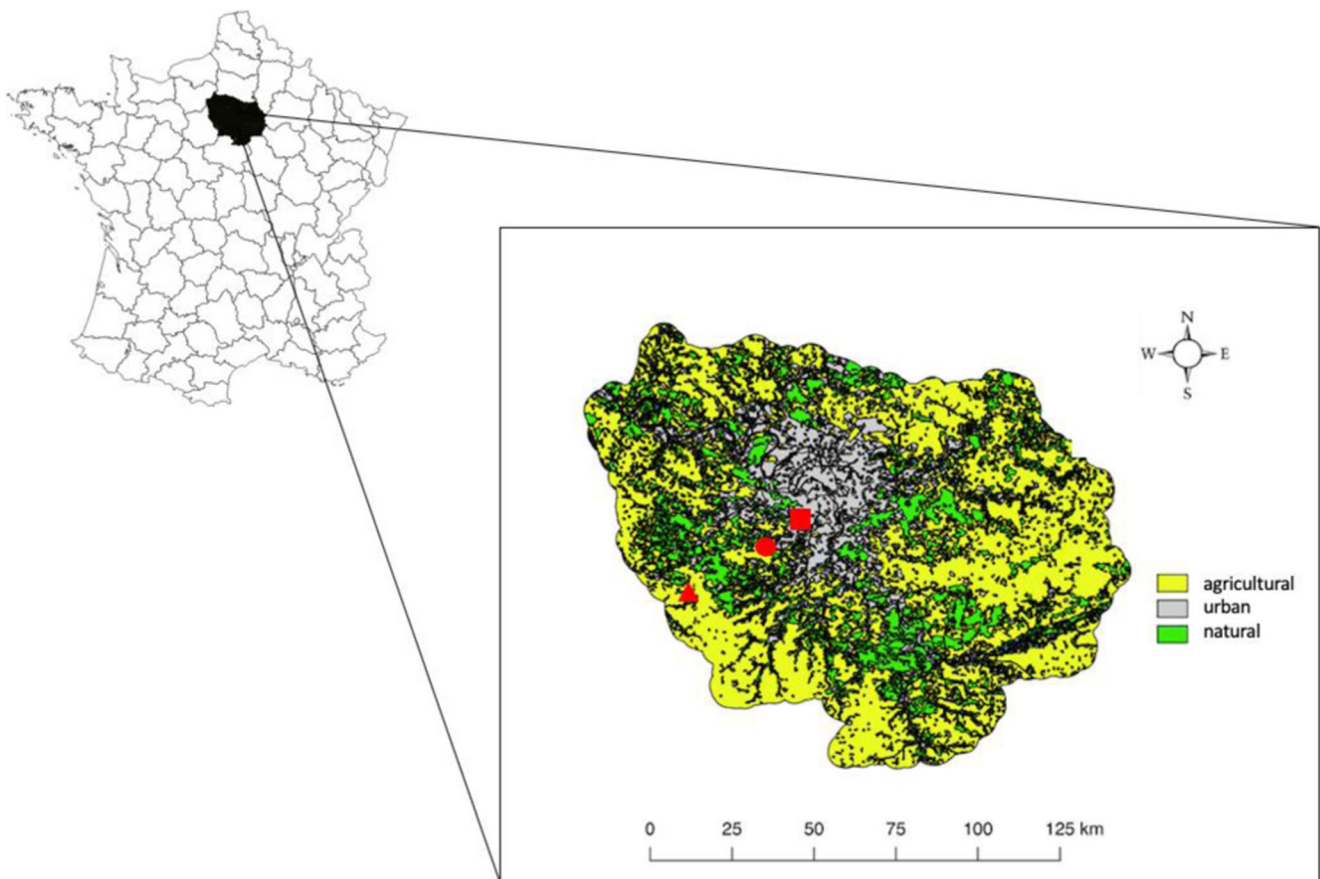
### Study sites

Red fox and domestic cat populations were non-invasively monitored by collecting faecal samples (hereafter, scats) at three suburban study sites (Fig. 1). Sceaux urban park (hereafter, park) (48°46'03.17"N, 2°17'47.48"E), located 20 km south of Paris, covers an area of 1.81 km<sup>2</sup> and comprises three main habitat types: open areas (lawns and meadows), wooded areas (composed of 16% *Fraxinus* sp., 14% *Acer platanoides*, 12% *Acer pseudoplatanus*, and 9% *Carpinus*), and French formal gardens (predominately ornamental species) (Hauts-de-Seine Conseil Général 2015). The agricultural area of Saclay (hereafter, agricultural land) (48°42'32.18"N, 2°10'33.00"E) is located between the north of the Essonne department and the southeast of the Yvelines department. This fertile agricultural land extending over 27 km<sup>2</sup> has a long agricultural

tradition with the primary crops of colza, wheat, and barley. Currently, this area is facing urbanisation pressure due to the development of a university and laboratory cluster (Spaak 2013). Rambouillet forest (hereafter, forest) (48°40'29.84"N, 1°48'27.17"E), located in the south of the Yvelines department, is one of the largest forests in the Île-de-France region. This wooded area of 200 km<sup>2</sup>, mainly composed of oaks and coniferous (68% and 25%, respectively), covers a territory of 29 municipalities (Ministère de l'agriculture et de la pêche 2015).

### Sampling protocol

One month prior to the start of predator scat sampling, all study sites were cleaned by removing old scats. Scat sampling was carried out four times per year in the middle of each season (October/autumn; January/winter; April/spring; July/summer) over two consecutive years (2014–2016) for each of the three study sites. Carnivora scats are cylindrical (i.e., sausage-shaped) with sub-division tapped at one of the extremities (Chame 2003). These characteristics may therefore promote scat misidentifications among mammalian carnivores of similar body size (Reid 2015; Morin et al. 2016). Red fox and domestic cat scats, however, can be differentiated by their morphometry (Bang and Dahlström 1975) and secondarily by their place of deposition, dietary content, and odour. Red fox scats (8–10 cm length and 2 cm width) are larger than those of domestic cats (6–8 cm length and 1–1.5 cm width) (Chame 2003). Moreover, red fox scats are tubular, long, and twisted with pointed ends, whereas domestic cat scats are smoothed and compacted with well-defined segments and only one tapered extremity (Chame 2003). Red foxes usually deposit scats in prominent positions along tracks to signal their presence to other individuals, whereas domestic cats tend to bury theirs (Seton 1925, Gibbons 2003). Regarding dietary contents, domestic cat scats strictly reflect their carnivorous diet with the additional presence of grass leaves ingested to aid hair elimination and/or Gramineae seeds indirectly ingested with the grass leaves (Chame 2003). Fresh red fox scats present a strong “foxy” smell like middle skunk (Gibbons 2003). Scats were collected by walking along the same paths in each study site and season. They were individually geolocalised, stored in separate plastic bags, and frozen (− 20 °C) until analysis. In this study, we aimed to detect the heterogeneity of predator diet in the main suburban habitats and across seasons. Thus, though informative, within-habitat site replications were not assessed; indeed, this was not possible in the park and agricultural land due to their limited areas. Because of the low number of domestic cat scats collected in the forest and park, we asked volunteer owners to collect the scats of their own vagrant cats during each study period. Four owners from each study site (forest and park) with one to three cats in their house collaborated with us.



**Fig. 1** Location of three study sites (park = square, agricultural land = circle and forest = triangle) where red fox and domestic cat scats were recovered during two-years of field work over three main land cover use (agricultural, urban and natural) reclassified from Corine Land Cover 2012

Due to the small number of red fox and domestic cat scats containing prey remains in some seasons and years, we decided to pool samples by season (i.e., without considering the year). Only seasons with at least 10 scats with prey remains per predator species were included in the following analyses (Table S1). Despite the collaboration of cat owners, many of the collected scats did not contain any prey remains. As a result, we did not have sufficient numbers of cat scats from the park for all seasons or from the forest in spring to include them in the analyses (Table S1).

### Laboratory analyses

Scats were analysed macroscopically and microscopically. Macroscopic analysis was performed by washing the scats individually under a stream of water in a 2  $\mu\text{m}$  sieve. We excluded scats without prey remains (i.e., feathers, hairs, bones, seeds). Prey remains were identified under a binocular to the finest taxonomic level possible using the bone reference collections from the National Museum of Natural History in Paris for mammals and birds, and identification keys for invertebrates and fruits before validating our identifications with specialists of the targeted

groups. Indigestible prey remains (e.g., hair, teeth, bones, skin, scales, feathers, exoskeletons, seeds from fleshy fruits) were then classified into 16 main food categories for a more accurate diet comparison: Microtidae (including *Myodes glareolus*, *Microtus agrestis*, and *Microtus arvalis*), Muridae (including *Apodemus sylvaticus*, *Mus musculus*, *Rattus sp.*, *rattus norvegicus*, and *Rattus rattus*), Soricidae (including *Sorex coronatus*, *Crocidura leucodon*, and *Crocidura russula*), Leporidae (including *Oryctolagus cuniculus* and *Lepus europaeus*), small birds (~ size of Passeroidea), large-medium birds (~ size of Corvoidea), Coleoptera, Hymenoptera, Dermaptera, Orthoptera, Heteroptera, Lepidoptera, Arachnida, earthworms, small fruits (*Prunus cerasus*, *P. prunus*, and *Rubus ulmifolius*), and large fruits (*Malus sp.* and *Pyrus sp.*). We also reported the frequency of nonorganic (e.g., plastic, foil paper) anthropogenic refuse (hereafter, refuse). Coprophagous, recycling, and ticks were excluded from the invertebrate prey.

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

## Data analyses

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

(i) *no.chaetae in scat*

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

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

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

To quantify the ingested prey biomass contained in each scat ( $prey_{IBS}$ ), we firstly calculated the total ingested biomass (TIB) by multiplying the  $prey_{MNI}$  of each prey by its mean mass (MM). The biomass of small mammals ( $MM = 57.32$  g) and birds ( $MM = 302.54$  g) was calculated using weight data extracted from the Amniote trait database (Myhrvold et al. 2015). We estimated invertebrate MM by weighing field-collected individuals from the orders most commonly consumed by the studied predators: Coleoptera ( $n = 156$ ,  $MM = 0.29$  g), Hymenoptera ( $n = 26$ ,  $MM = 0.01$  g), Dermaptera ( $n = 20$ ,  $MM = 0.03$  g), Orthoptera ( $n = 71$ ,  $MM = 0.10$  g), Heteroptera ( $n = 76$ ,  $MM = 0.02$  g), and Lepidoptera ( $n = 92$ ,  $MM = 0.02$  g), as well as the class Arachnida ( $n = 87$ ,  $MM = 0.01$  g). Fruit MM was obtained by collecting and weighing the following fruits from the study sites: *Rubus ulmifolius* ( $n = 150$ ,  $MM = 2.19$  g), *Prunus prunus* ( $n = 39$ ,  $MM = 15.09$  g), *P. cerasus* ( $n = 30$ ,  $MM = 3.70$  g), *Malus* sp. ( $n = 73$ , mean  $MM = 90.01$  g), and *Pyrus* sp. ( $n = 71$ ,  $MM = 98.55$  g). Since red foxes and domestic cats are known to ingest large body mass prey (e.g., Leporidae, large birds) only partially (Artois 1989; Bonnaud et al. 2007), we estimated the ingested proportion of lagomorphs and large-medium birds by calculating the maximum food intake per scat of each predator. To do so, we selected red fox ( $n = 75$ ) and domestic cat ( $n = 53$ )

scats containing only small mammals (i.e., prey entirely ingested) and multiplied their  $prey_{MNI}$  by their MM to obtain a maximum ingested biomass (MIB in g of fresh biomass) for each predator scat. MIB was 244.09 g and 232.40 g for red fox and domestic cat, respectively. We then calculated the ingested biomass of each prey category per scat ( $prey_{IBS}$ ) by using one of the two following formulas. If the TIB did not exceed the MIB, we applied the formula:

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

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

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

Where  $\text{RIB}_j$  is the relative ingested biomass of each large prey calculated as follows:

$$(vi) \text{RIB}_j = \frac{\left( \text{large prey}_j \text{biomass} \times \text{large prey}_j \text{number} \right)}{\sum_1^n \left( \text{large prey}_j \text{biomass} \times \text{large prey}_j \text{number} \right)}$$

## Effects of study sites and seasons on predator diet

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

## Predator diet breadths and overlaps

We used  $prey_{MNI}$  to calculate the degree of trophic specialisation for each studied predator by estimating their diet breadth



(B) and degree of diet overlap (O) using the *nichevar* and *nicheoverlap* functions from the *indicpecies* package, respectively (Caceres and Legendre 2009). Diet breadth ranges from 0 to 1, with values close to 0 for specialised populations and values close to 1 for generalists. Diet overlap ranges from 0 to 1, with values close to 0 for low diet overlap between predator populations and values close to 1 for high diet overlap.

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

## Results

In total, we collected 1073 scats, but 332 did not contain any wild prey remains (i.e., only highly digestible organic matter like industrial food and/or refuse), with 55% of them belonging to red foxes (park:  $n = 94$ , agricultural land:  $n = 24$ , managed forest:  $n = 65$ ) and 45% to domestic cats (park:  $n = 85$ , agricultural land:  $n = 21$ , managed forest:  $n = 43$ ) (Table S1). From the remaining 741 scats containing prey remains, 74% belonged to red foxes (park:  $n = 220$ , agricultural land:  $n = 159$ , managed forest:  $n = 169$ ) and 26% to domestic cats (park:  $n = 0$ , agricultural land:  $n = 146$ , managed forest:  $n = 47$ ) (Table S1). Out of these 741 scats, 41 scats contained prey remains that were not attributable to the 16 main prey groups defined above (e.g., scats containing unidentifiable parts of invertebrates, seeds, feathers, or hairs). This resulted in the inclusion of 700 scats in  $\text{prey}_{\text{IBS}}$  and  $\text{prey}_{\text{MNI}}$  models, corresponding to 699 degrees of freedom in general models and 521 and 177 degrees of freedom in red fox ( $n = 522$ ) and domestic cat ( $n = 178$ ) models, respectively.

We identified a total of 6742 prey items. Based on  $\text{prey}_{\text{IBS}}$ , red fox diet was mainly composed of Rodentia (37%) and large-medium birds (28%), and domestic cat diet of Leporidae (41%) and large-medium birds (27%) (Table 1). Based on the  $\text{prey}_{\text{MNI}}$ , red fox diet was mainly composed of earthworms (53%), and domestic cat diet of earthworms (40%) and Microtidae (21%) (Table 1).

The composition of both predators' diets ( $\text{prey}_{\text{IBS}}$ ) was influenced by predator species, study sites, seasons, and the interaction between study sites and seasons (Table S2a). Predator species affected diet  $\text{prey}_{\text{IBS}}$  in terms of Leporidae, Microtidae, Coleoptera, earthworms, and small fruits. Study site affected both predators' consumption of Leporidae, Microtidae, Muridae, Soricidae, large-medium birds, Coleoptera, and earthworms. Seasons influenced both predators' diets in terms of Coleoptera, earthworms, and small

fruits. The interaction between study site and season also affected both predators' diets in terms of Leporidae, large-medium birds, Coleoptera, and small fruits (Table S2a).

### Red fox diet

The composition of red fox diet ( $\text{prey}_{\text{IBS}}$ ) was influenced by study sites, seasons, and the interaction between study sites and seasons (Table 2a). Study site affected red fox  $\text{prey}_{\text{IBS}}$  in terms of Microtidae, Muridae, large-medium birds, Coleoptera, earthworms, and small fruits. Seasons influenced red fox consumption of Coleoptera, earthworms, and small fruits. The interaction between study site and season also affected red fox  $\text{prey}_{\text{IBS}}$  in terms of large-medium birds, Coleoptera, and small fruits (Table 2a).

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

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

### Domestic cat diet

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

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

Based on the minimum number of ingested individuals ( $\text{prey}_{\text{MNI}}$ ), in agricultural land, domestic cat diet was mainly composed of earthworms (48%), particularly in autumn (60%), winter (64%), and spring (34%), followed by

**Table 1** Minimum number of individual prey in each scat ( $prey_{MNI}$ ) and ingested prey biomass in each scat ( $prey_{IBS}$ ) (in brackets) divided by total  $prey_{MNI}$  and  $prey_{IBS}$  respectively. Data is expressed in percentage by predator species (red fox, domestic cat), study sites (park, agricultural land, forest) and seasons (autumn, winter, spring, summer)

habitat	park				agricultural land				forest			
	autumn	winter	spring	summer	autumn	winter	spring	summer	autumn	winter	spring	summer
predator	red fox											
Leporidae	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.29 (10.35)	1.81 (37.4-0)	1.03 (19.6-0)	0.51 (11.70)	1.61 (29.99)	0.96 (48.71)	0.57 (26.1-1)	0.49 (98.4-8)	0.27 (19.95)
Microtidae	0.17 (1.09)	0.33 (0.00)	0.43 (0.00)	0.29 (0.21)	2.54 (0.49)	18.47 (7.86)	19.41 (12.35)	9.24 (4.44)	0.48 (0.00)	4.90 (6.03)	1.23 (0.00)	5.20 (11.05)
Muridae	0.171 (0.00)	0.33 (0.00)	0.43 (0.00)	0.14 (0.28)	0.36 (1.45)	3.08 (15.2-9)	5.11 (29.94)	2.41 (9.93)	0.48 (0.00)	5.65 (52.7-3)	0.49 (0.00)	1.64 (15.92)
Soricidae	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.51 (0.00)	1.02 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	1.64 (0.00)
Rodentia	0.69 (25.0-0)	2.01 (7.27)	0.85 (0.89)	0.58 (0.64)	4.35 (3.29)	3.08 (2.74)	0.51 (0.00)	2.28 (2.67)	1.44 (4.08)	1.32 (0.00)	1.23 (1.09)	4.10 (1.78)
LM birds	0.26 (72.9-2)	0.00 (0.00)	4.26 (98.9-7)	1.66 (60.22)	2.54 (49.9-9)	1.03 (12.8-3)	1.02 (23.43)	2.55 (37.23)	0.00 (0.00)	0.38 (11.4-1)	0.00 (0.00)	0.55 (38.01)
Small birds	0.51 (0.00)	0.33 (0.00)	0.85 (0.00)	0.58 (0.00)	0.73 (0.00)	0.51 (0.00)	1.02 (0.00)	1.21 (0.44)	0.96 (0.00)	0.94 (0.00)	0.74 (0.00)	0.00 (0.00)
Birds unidentified	0.00 (0.00)	0.67 (85.0-6)	0.00 (0.00)	0.50 (13.20)	0.73 (7.28)	2.05 (39.3-9)	1.53 (21.31)	0.54 (5.73)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.27 (13.03)
Coleoptera	1.03 (0.00)	0.67 (0.04)	3.40 (0.03)	12.54 (0.08)	0.00 (0.00)	1.54 (0.00)	2.55 (0.00)	5.36 (0.02)	0.00 (0.00)	5.65 (0.08)	29.32 (0.06)	41.29 (0.01)
Hymenoptera	0.51 (0.00)	0.00 (0.00)	0.85 (0.00)	2.38 (0.00)	0.00 (0.00)	0.00 (0.00)	2.55 (0.00)	3.89 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.82 (0.00)
Dermaptera	4.46 (0.00)	2.01 (0.00)	0.85 (0.00)	0.87 (0.00)	0.36 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.19 (0.00)	0.00 (0.00)	1.37 (0.00)
Orthoptera	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.07 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.13 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.82 (0.00)
Heteroptera	0.17 (0.00)	0.00 (0.00)	0.00 (0.00)	0.58 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.27 (0.00)	0.00 (0.00)	0.00 (0.00)	0.25 (0.00)	0.00 (0.00)
Lepidoptera	1.46 (0.00)	0.67 (0.00)	0.85 (0.00)	1.08 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	1.44 (0.00)	0.00 (0.00)	2.46 (0.00)	0.55 (0.00)
Arachnida	0.09 (0.00)	2.34 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.27 (0.00)
Earthworms	89.64 (1.00)	76.95 (4.97)	87.14 (0.11)	29.77 (0.42)	61.36 (0.02)	36.15 (1.77)	64.03 (0.48)	14.49 (0.04)	26.12 (0.00)	79.42 (1.01)	63.78 (0.37)	29.18 (0.00)
Invert. unidentified	0.51 (0.00)	0.00 (0.00)	0.00 (0.00)	0.14 (0.00)	0.00 (0.00)	2.05 (0.02)	0.51 (0.00)	0.40 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.82 (0.00)
Small fruits	0.09 (0.00)	13.38 (0.00)	0.00 (0.00)	48.45 (14.40)	24.68 (0.08)	30.28 (0.37)	0.00 (0.00)	55.46 (9.41)	63.42 (22.11)	0.19 (0.02)	0.00 (0.00)	11.20 (0.25)
Large fruits	0.23 (0.00)	0.30 (2.66)	0.09 (0.00)	0.08 (0.00)	0.54 (0.00)	0.22 (0.13)	0.22 (0.80)	0.17 (0.09)	4.70 (25.00)	0.80 (2.61)	0.00 (0.00)	0.00 (0.00)
Refuse*	0.00	6.45	7.69	8.04	0.00	0.00	0.00	2.74	0.00	2.50	0.00	1.33
predator	domestic cat											
Leporidae	–	–	–	–	8.95 (66.5-8)	5.33 (52.0-6)	16.15 (77.08)	7.71 (36.64)	2.49 (33.33)	2.16 (33.3-3)	–	0.00 (0.00)
Microtidae	–	–	–	–	14.64 (0.31)	15.58 (0.56)	21.54 (0.55)	33.72 (2.41)	2.49 (0.00)	30.19 (0.00)	–	51.76 (16.01)
Muridae	–	–	–	–	3.25 (0.31)	2.46 (1.62)	4.04 (0.27)	12.52 (6.08)	2.49 (0.00)	2.16 (0.00)	–	27.06 (69.53)

**Table 1** (continued)

habitat	park				agricultural land				forest			
	autumn	winter	spring	summer	autumn	winter	spring	summer	autumn	winter	spring	summer
Soricidae	–	–	–	–	0.00 (0.00)	0.00 (0.00)	1.35 (0.00)	3.85 (0.09)	0.00 (0.00)	4.31 (0.00)	–	0.00 (0.00)
Rodentia	–	–	–	–	3.25 (6.25)	3.28 (0.58)	4.04 (0.00)	2.89 (0.34)	0.00 (0.00)	6.47 (2.98)	–	0.00 (0.00)
LM birds	–	–	–	–	4.07 (26.1- 0)	4.92 (44.6- 3)	6.73 (19.73)	10.60 (47.16)	0.00 (0.00)	4.31 (63.6- 8)	–	1.18 (9.13)
Small birds	–	–	–	–	0.00 (0.00)	2.46 (0.00)	5.38 (0.11)	1.93 (0.30)	2.49 (0.00)	0.00 (0.00)	–	2.35 (0.00)
Birds unidentified -	–	–	–	–	0.00 (0.00)	0.41 (0.48)	1.35 (2.21)	1.93 (6.89)	4.97 (66.67)	0.00 (0.00)	–	1.18 (5.27)
Coleoptera	–	–	–	–	2.44 (0.00)	0.82 (0.00)	5.38 (0.00)	6.74 (0.01)	14.91 (0.00)	0.00 (0.00)	–	10.59 (0.04)
Hymenoptera -	–	–	–	–	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	5.78 (0.00)	0.00 (0.00)	0.00 (0.00)	–	0.00 (0.00)
Dermaptera	–	–	–	–	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	–	0.00 (0.00)
Orthoptera	–	–	–	–	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.96 (0.00)	0.00 (0.00)	0.00 (0.00)	–	4.71 (0.00)
Heteroptera	–	–	–	–	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	–	0.00 (0.00)
Lepidoptera	–	–	–	–	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	–	0.00 (0.00)
Arachnida	–	–	–	–	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	–	0.00 (0.00)
Earthworms	–	–	–	–	60.32 (0.07)	64.47 (0.08)	34.04 (0.04)	4.19 (0.02)	65.21 (0.00)	47.44 (0.00)	–	1.18 (0.02)
Invert. unidentified -	–	–	–	–	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	2.89 (0.00)	0.00 (0.00)	0.00 (0.00)	–	0.00 (0.00)
Small fruits	–	–	–	–	1.63 (0.00)	0.00 (0.00)	0.00 (0.00)	3.85 (0.05)	4.97 (0.00)	0.08 (0.00)	–	0.00 (0.00)
Large fruits	–	–	–	–	1.44 (0.37)	0.27 (0.00)	0.00 (0.00)	0.43 (0.00)	0.00 (0.00)	2.88 (0.00)	–	0.00 (0.00)
Refuse*	0.00	0.00	0.00	0.00	10.00	0.00	0.00	0.00	13.33	0.00	0.00	0.00

\*percentage of scats with presence of non-organic refuse (i.e., plastic, foil paper)

Microtidae (20%), especially in summer (34%) (Table 1). In the forest, domestic cat diet mainly comprised earthworms (22%), particularly in autumn (65%) and winter (47%), followed by Microtidae (22%), especially in summer (52%) (Table 1).

### Diet breadth and overlap

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

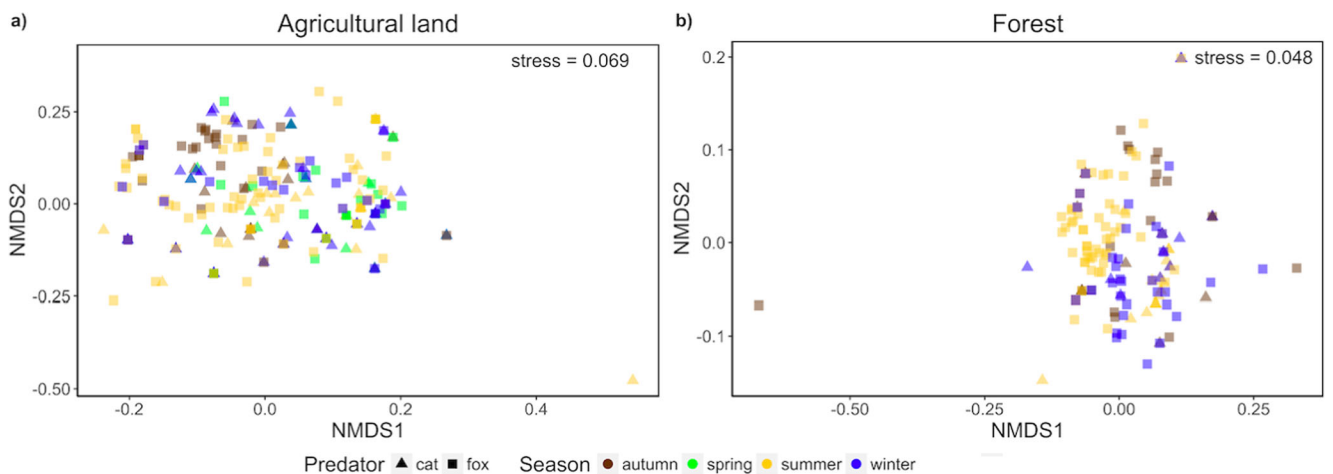
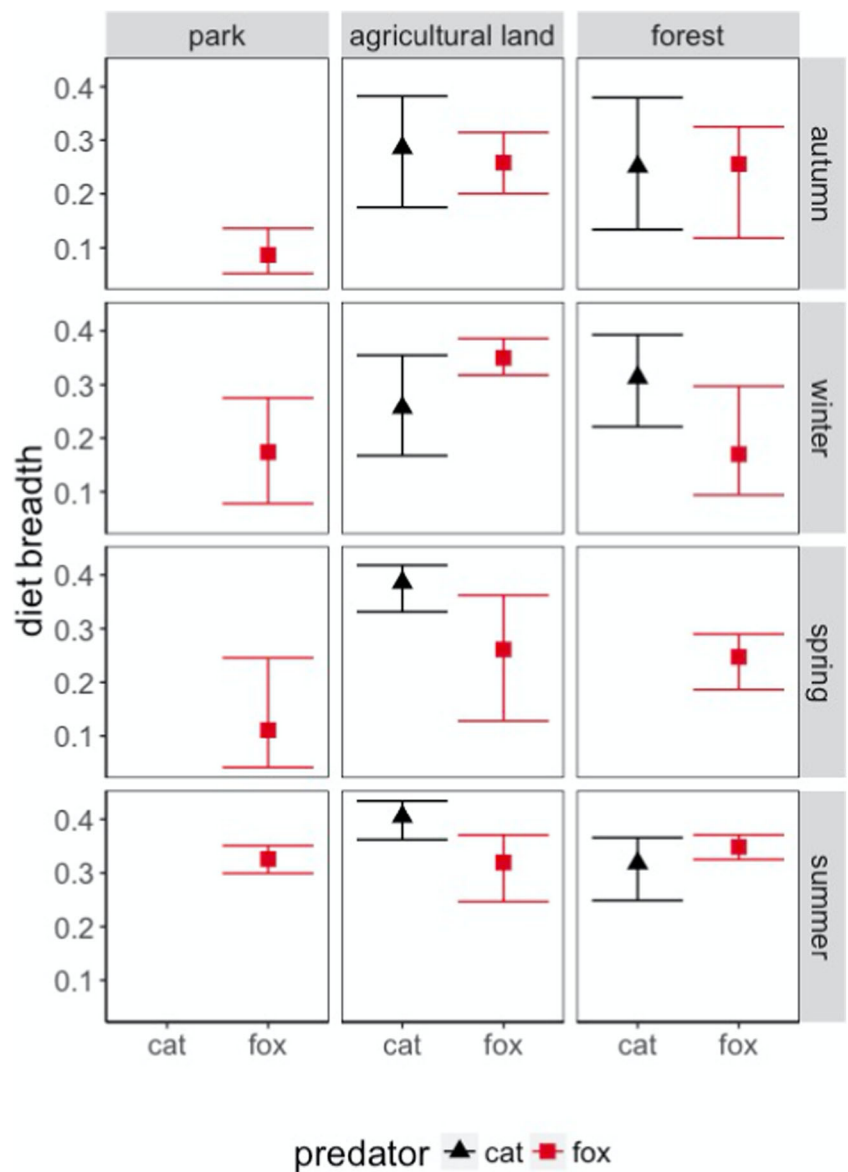
Interestingly, in agricultural land, we found a high degree of diet overlap between red fox and domestic cat populations across all seasons ( $O > 0.75$ ) except summer ( $O = 0.33$ , 95% CI [0.20, 0.56]) (Table S4). During this season, dissimilarity between red fox and domestic cat diet (i.e., points located far from each other with little or no overlap) was higher compared to the other seasons (Fig. 3a). By contrast, we detected higher variations in the diet overlap between red fox and domestic cat populations in the forest compared to agricultural land, with the highest value found in winter ( $O = 0.92$  95% CI [0.05, 0.99]) and the lowest in summer ( $O = 0.25$  95% CI [0.04, 0.60]) (Table S4). In winter, red fox and domestic cat diet showed the highest similarity (i.e., most points are spatially close to each other or overlapping), while the lowest diet similarity was observed in summer (Fig. 3b). Due to the limited

**Table 2** Multivariate Generalized Linear Model results of red fox diet (a) and domestic cat (b) composition (prey<sub>IBS</sub>) across study sites (park, agricultural land and forest) and seasons (autumn, winter, spring and summer). Res.df = residual degrees of freedom, df = degree of freedom, Dev = deviation test statistic, Pr = *p* value. *P*-values were calculated using 999 resampling iterations via PIT-trap resampling (to account for correlation in testing). Bold indicates *p* < 0.05

Multivariate test:			Muridae		Soricidae		Large-medium birds		Small birds		Coleoptera		Hymenoptera	
	Res.Df	Df.diff	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)
intercept	521													
site	519	2	135.6	<b>0.001</b>										
season	516	3	187.4	<b>0.001</b>										
site: season	510	6	210.6	<b>0.001</b>										
Univariate tests:														
	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)
intercept	2.689	0.133	41.774	<b>0.001</b>	5.904	<b>0.019</b>	7.308	<b>0.019</b>	0.135	0.731	43.400	<b>0.001</b>	0.000	1.000
site	0.730	0.756	4.756	0.428	2.041	0.751	0.883	0.756	1.061	0.753	43.284	<b>0.001</b>	0.000	1.000
season	13.497	0.221	5.738	0.671	4.062	0.671	26.131	<b>0.003</b>	13.488	0.221	23.043	<b>0.015</b>	0.000	1.000
site: season	Dev	Pr(>Dev)	Orthoptera		Heteroptera		Arachnida		Earthworms		Small fruits		Large fruits	
intercept	1.792	0.562	0.000	1.000	0.000	1.000	0.000	1.000	16.667	<b>0.001</b>	7.354	<b>0.019</b>	0.942	0.562
site	2.976	0.751	0.000	1.000	0.000	1.000	0.000	1.000	40.795	<b>0.001</b>	81.679	<b>0.001</b>	6.704	0.203
season	0.004	0.671	0.000	1.000	0.000	1.000	0.000	1.000	9.135	0.513	89.212	<b>0.001</b>	14.823	0.192
site: season														
b) Multivariate test:														
	Res.Df	Df.diff	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)
intercept	177													
site	175	2	8.36	0.232										
season	172	3	43.90	<b>0.001</b>										
site: season	171	2	37.50	<b>0.003</b>										
Univariate tests:														
	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)
intercept	3.176	0.369	1.703	0.725	1.62	0.725	0.885	0.896	0.001	0.998	0.329	0.973	0.000	1.000
site	2.231	0.811	3.451	0.811	2.731	0.811	0.735	0.919	1.576	0.877	0.98	0.919	0.000	1.000
season	9.179	0.060	4.132	0.469	0.427	0.933	5.023	0.371	5.886	0.334	0.704	0.933	0.000	1.000
site: season	Dev	Pr(>Dev)	Orthoptera		Heteroptera		Arachnida		Earthworms		Small fruits		Large fruits	
intercept	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.014	0.998	0.014	0.998	0.574	0.943
site	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	18.072	<b>0.001</b>	7.105	0.287	3.229	0.811
season	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.019	0.988	2.229	0.688	4.115	0.469
site: season														



**Fig. 2** Red fox and domestic cat mean diet breadth (95% CI) across habitats (park, agricultural land and forest) and seasons (autumn, winter, spring and summer). Only sample size larger than 10 scats collected per predator, site and season were analyzed



**Fig. 3** Nonmetric MultiDimensional Scaling (NMDS) plots, constructed from Bray-Curtis similarity matrices based on prey<sub>MNI</sub> data, showing diet composition of red foxes and domestic cats across seasons in studied

suburban habitats: a) agricultural land and b) forest. Only sample size larger than 10 scats collected per predator, site and season were analyzed

number of collected cat scats in some habitats and seasons, we did not calculate the diet overlap between red fox and domestic cat populations in the forest in spring or in the park for all seasons.

## Discussion

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

### Red fox and domestic cat diets

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

The trophic index based on the minimum number of ingested individuals ( $\text{prey}_{\text{MNI}}$ ) revealed that earthworms were the most abundantly consumed prey in red fox diet. This result is in good agreement with other studies once refuse is removed from red fox diet (MacDonald 1980; Harris 1981; Doncaster et al. 1990; Reynolds and Aebischer 1991; Saunders et al. 1993; Soulsbury et al. 2008). In domestic cat diet, earthworms along with Microtidae were the most abundantly consumed prey. While the presence of chaetae in predator scats may be increased by phenomena such as soil contamination and secondary predation (i.e., chaetae would have persisted after two digestions), potentially leading to a slight overestimation of earthworm consumption, the high number of consumed earthworms stresses the importance of this prey type for both red foxes and domestic cats, as it may supply these predators with their protein requirements within human-dominated landscapes. Even if striking, the consumption of earthworms (protein-rich prey) by domestic cats is probably

opportunistic and focussed on anecic and/or epigeic earthworms (Lee 1985), which are readily available and easy to catch in agricultural and forest soils. This interesting result should be confirmed (i.e., earthworm species identification) in future studies using metabarcoding approaches, for example (Bienert et al. 2012; Boyer et al. 2013; Pansu et al. 2015). In general, the macro- and microscopic diet analyses of predator diets would benefit from metabarcoding approaches to verify prey identification, detect and identify digested soft-bodied prey (e.g., insect larvae, egg content), and confirm predator scat identification (Pompanon et al. 2012; Galan et al. 2018).

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

Red fox populations showed study site specificities in terms of the proportion of ingested biomass for certain prey categories (Microtidae, Muridae, large-medium birds, Coleoptera, earthworms, and small fruits) as well as seasonal dietary shifts for some of these resources (Coleoptera, earthworms, and small fruits) (Tables 1 and 2a).

These results are in good agreement with and support the generalist and opportunistic trophic behaviour of red foxes (Sillero et al. 2004). Thanks to this trophic behaviour, red foxes could adapt their diet in contrasting human-dominated landscapes according to the abundance and availability of associated prey communities and fruit resources (e.g., emergence of Coleoptera, fructification of fleshy fruits) (Díaz-Ruiz et al. 2013).

In contrast to red fox diet, domestic cat diet (in terms of ingested prey biomass) was relatively homogeneous across study sites and mainly focussed on mammals (Leporidae and Muridae; Gillies and Fitzgerald 2005 (New Zealand); Kays and Dewan 2004 (US); Krauze-Gryz et al. 2012 (Europe)) and secondarily on large-medium birds, with only the proportion of ingested earthworm biomass changing seasonally (Tables 1 and 2b). This suggests that cats are highly adaptable and efficient hunters, which allows them to survive and reproduce without regard to the type of habitat, thus confirming the opportunistic but strictly carnivore trophic behaviour of domestic cats (Bradshaw et al. 1996; Medina et al. 2011). By consequence, the increased number of vagrant domestic cats due to the higher human population density can lead to negative effects on bird, mammal, and reptile population dynamics in many different types of habitats (Woods et al. 2003; Dauphiné and Cooper 2009; Blancher 2013; Loss et al. 2013; Doherty et al. 2015). As the opportunistic behaviour of these predators likely depends on resource abundance and availability, which are rarely monitored and quantified, this should be investigated in future studies to detect potential patterns of prey preferences.

At all the study sites, both red foxes and domestic cats abundantly consumed earthworms (in prey<sub>MNI</sub>) in autumn, winter, and spring, probably due to the scarcity of other prey categories during these seasons of relatively low productivity. The use of this alternative high-protein prey may allow red foxes and domestic cats to maintain stable populations all year round within degraded human-dominated landscapes. Interestingly, in agricultural land, domestic cats turned to the consumption of *Microtus agrestis* individuals as observed in other rural areas in Europe (Krauze-Gryz et al. 2012), while red foxes shifted their diet to temporarily abundant small fruits that are rich in carbohydrates, minerals, and vitamins (e.g., *Prunus cerasus*, *P. prunus*, *Rubus ulmifolius*) (Table 1). Red fox consumption of fruits has already been described in other studies in Europe (Contesse et al. 2004) and Asia (Dell'Arte et al. 2005; Ghoshal et al. 2016). In addition to being an alternative source of nutrient for foxes, these fruits contained seeds that can be efficiently dispersed (Herrera 1989; Matías et al. 2010), leading to the conservation of the vegetation structure of these habitats. Last but not least, the consumption of voles by domestic cats in summer likely corresponds to a peak abundance of this prey, which supports the opportunistic trophic behaviour of cats. As domestic cats are one of the major predators of voles (Lin and Batzli 1995), they could modify the cyclicality of the prey population dynamics (Hansson 1988) and indirectly affect the trophic behaviour of other predators sharing this prey such as red foxes.

### Diet breadth and overlap

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

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

These are the first results regarding the degree of diet overlap between red foxes and domestic cats within human-dominated landscapes, which are in good agreement with those found in natural habitats (Paltridge 2002; Woinarski et al. 2017). In our study, in summer, red fox and domestic cat diets only marginally overlapped, suggesting that they can hunt a wider prey spectrum to reduce their degree of trophic overlap through niche partitioning. On the contrary, diet overlaps between red foxes and domestic cats were particularly high during the less productive seasons (i.e., autumn, winter,

and spring) when they have to share scarcer main and alternative prey (i.e., mammals, birds, and earthworms). This indicates that competition between red foxes and domestic cats may occur, particularly if these predators are in high abundance in city centres (Šálek et al. 2015; Flockhart et al. 2016) and probably more broadly in human-dominated areas. However, competition for food between species is eased by their generalist behaviour. In addition, these high seasonal diet overlaps between red foxes and domestic cats may exacerbate their predation pressure over shared prey populations and can lead to potential negative effects on shared prey population dynamics. To quantify predation impacts on prey population dynamics, future studies should simultaneously monitor predator diets as well as prey and predator availabilities through space and time.

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**Author's contributions** IC collected and analysed the data and led the writing of the manuscript. DZL contributed to performing the diet descriptors. EB conceived the ideas and designed the methodology. All authors contributed to the writing and gave their final approval for publication.

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