

1 Fine-scale variation within urban landscapes affects
2 marking patterns and gastrointestinal parasite diversity
3 in red foxes.

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20 Key words

21 gastrointestinal parasites; landscape fragmentation; urban disease ecology; urban ecology;
22 urban carnivores; *Vulpes vulpes*;

Abstract

1. Urban areas are often considered to be a hostile environment for wildlife as they are highly fragmented and frequently disturbed. However, these same habitats can contain abundant resources, while lacking many common competitors and predators. The urban environment can have a direct impact on the species living there but can also have indirect effects on their parasites and pathogens. To date, relatively few studies have measured how fine-scale spatial heterogeneity within urban landscapes can affect parasite transmission and persistence.
2. Here we surveyed 237 greenspaces across the urban environment of Edinburgh (UK) to investigate how fine-scale variation in socio-economic and ecological variables can affect red fox (*Vulpes vulpes*) marking behaviour, gastrointestinal (GI) parasite prevalence and parasite community diversity,
3. We found that the presence and abundance of red fox faecal markings was non-uniformly distributed across greenspaces, and instead was dependent on the ecological characteristics of a site. Specifically, common foraging areas were left largely unmarked, which indicates that suitable resting and denning sites may be limiting factor in urban environments. In addition, the amount of greenspace around each site was positively correlated with overall GI parasite prevalence, species richness and diversity, highlighting the importance of greenspace (a commonly used measure of landscape connectivity) in determining the composition of the parasite community in urban areas.
4. Our results suggest that fine scale variation within urban environments can be important for understanding the ecology of infectious diseases in urban wildlife and could have wider implication for the management of urban carnivores.

47 Introduction

48 Urban areas are expanding around the world due to both the increase in overall human
49 population size and the trend of migration from the countryside to larger settlements (United Nations,
50 2008). These urbanised areas can represent “virgin” ecosystems, as they often are devoid of resident
51 species, which can be a challenging environment for wildlife (McIntre *et al.*, 2000; Lowry *et al.*, 2013).
52 In addition, urban habitats are highly disturbed and can be very fragmented (Fernandez-Juricic, 2000);
53 due to traffic (Magle *et al.*, 2009), noise pollution (Francis *et al.*, 2011), light pollution (Miller, 2006),
54 and the presence of people (Schlesinger *et al.*, 2008). While these conditions may provide challenges
55 for most wildlife species, urban areas also tend to have very abundant and stable food sources
56 (McKinney, 2006) and fewer predators and competitors than wild habitats (Crooks & Soulé, 1999).
57 Due to these unique ecological conditions, relatively few species have successfully adapted to exist,
58 and in many cases thrive, in urban environments (Lowry *et al.*, 2013); with the classic examples of
59 pigeons and rats (Luniak, 2004).

60 Ecological species assemblages, or communities, that exist in urban environments tend to
61 have a different composition from those found in wild settings (Aronson *et al.*, 2016), but they are not
62 necessarily less diverse (Parsons *et al.*, 2018). Urban communities often consist of species capable of
63 tolerating highly disturbed habitats, and able to exploit novel resources (Luniak, 2004). While there is
64 an increasing focus on understanding the ecological communities that emerge in urban areas, the
65 consequences for how the urban landscape may affect the parasite community remains unclear
66 (Bradley & Altizer, 2006). For this reason understanding the factors driving parasite diversity, infection
67 risk and parasite burdens in urban wildlife can be important to unravel the dynamics of transmission
68 at the wildlife-human and urban-wild interfaces (Gortázar *et al.*, 2007). For example, fragmented
69 landscape and the associated decrease in biodiversity found in urban areas is correlated with an
70 increase in the density of white-footed mice (*Peromyscus leucopus*), hosts for the spirochete bacteria
71 (*Borrelia burgdorferi*) that causes Lyme disease. Moreover, urbanisation can provide suitable habitat

to some species that would not normally live in close proximity with humans, increasing the risk of cross species or zoonotic transmission (Hassell *et al.*, 2017). For example, the presence of flying foxes (*Pteropus*) in urban areas has been associated with the spillovers of Hendra virus to humans and domestic animals in Eastern Australia (Plowright *et al.*, 2011).

However, it is difficult to make general predictions about the impact of urbanisation on the structure and dynamics of parasite communities, because there is enormous variation in the physical and biological composition of urban areas, which leads to highly variable urban ecological communities (McKinney, 2006). Therefore patterns and drivers of parasite infection, burden and diversity are unlikely to be consistent across urban areas (Bradley & Altizer, 2006). A clear example of this variation has been demonstrated through the in-depth investigation of *Echinococcus multilocularis*, a tapeworm with a complex life cycle, which causes alveolar echinococcosis, a zoonotic disease of increasing importance for humans across Europe. Red foxes are a competent definitive host for *E. multilocularis* and the presence of high density fox populations in urban areas has sparked concern for public health in endemic regions (Mackenstedt *et al.*, 2014). In a review of *E. multilocularis* in urban fox populations, Deplazes *et al* (2004) concluded that urban foxes consumes a lower proportion of small rodents (the intermediate hosts), which leads to lower infection rate in urban foxes compared to rural settings. However, further work that included recent research from China and Japan found contrasting results; higher *E. multilocularis* prevalence was associated with more urbanised areas in rural China, a pattern that was driven by the presence of free-roaming dogs, a key definitive host for *E. multilocularis*, (Liccioli *et al.*, 2015).

These contrasting patterns highlight the importance of taking into account the specific characteristics of urban landscapes in determining their impact on host-parasite dynamics. However producing a comprehensive definition of urban areas, that incorporates this intrinsic variability, is difficult (Weeks, 2010). In fact, most studies use subjective classifications to identify specific environments within urban areas, generally defining urban vs rural areas (see for example Prange *et*

97 *al.*, 2003; Fischer *et al.*, 2005; Reperant *et al.*, 2007; Robardet *et al.*, 2008). However, “urban” and
98 “rural” landscapes are just ends of a continuous spectrum of urbanisation, and to understand the
99 dynamics and structure of parasites communities in urban environments, it is important to be able to
100 classify specific characteristics of urban areas, or the level of ‘urbanity’, along this spectrum. These
101 metrics need to be objective, quantitative and capture the heterogeneity and fragmentation of the
102 urban environment on a fine scale, while also being able to accurately characterise the rural-urban
103 transition within continuous, multivariate space.

104 Red foxes (*Vulpes vulpes*) are an extremely adaptable species (Harris & Baker, 2001), with a
105 generalist diet (Contesse, Hegglin, Gloor, Bontadina, & Deplazes, 2004), high reproductive potential
106 (Pagh *et al.*, 2018) and a flexible social system (Iossa, Soulsbury, Baker, & Harris, 2008); these traits
107 have allowed foxes to adapt to urban environments and quickly establish dense populations (Harris,
108 1981; Janko *et al.*, 2012). Records from the early 1900s in London, suggest that urban fox populations
109 were already well established (Teagle, 1967). Patterns of long-standing urban fox populations have
110 been reported in numerous countries, particularly in Canada, Australia, Japan and in mainland Europe
111 (Harris and Rayner, 1986; Adkins & Stott, 1998; Gloor *et al.*, 2001; Marks & Bloomfield, 2006; Uraguchi
112 *et al.*, 2014). However, urban foxes have often been regarded as pests because they can carry
113 important zoonotic diseases (e.g. rabies virus, *E. multilocularis*) which generate concern for public
114 health (Comte *et al.*, 2013; Laurimaa *et al.*, 2016; Reperant *et al.*, 2007).

115 Here, we developed a multivariate, continuous measure of ‘urbanity’ in order to investigate
116 the effect of fine scale habitat changes on the abundance of fox territorial marking and the
117 composition of their gastrointestinal (GI) parasite communities across Edinburgh, UK. To do this, we
118 conducted an extensive, non-invasive survey of public greenspaces across the entire urban area of
119 Edinburgh, recorded all red fox scats to identify fox distribution patterns, and identified and quantified
120 the GI parasite community. We used fine spatial scale metrics that included both human socio-
121 economic variables (i.e. human population density, traffic counts, greenspace, etc.) and ecological

122 variables (i.e. presence of other wildlife species, habitat characteristics, etc.), to capture the complex
123 biotic and abiotic structure of the urban environment and investigate their relationship with parasite
124 diversity and infection prevalence. Our goal was to identify variables drive patterns of GI parasite
125 infection in the urban landscape, in order to provide an objective and easily quantifiable measure of
126 urbanity, as to improve comparability and repeatability of urban disease ecology studies.

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Methods

Study area and survey design

Fieldwork was carried out in the urban area of Edinburgh, United Kingdom (55.9533° N, 3.1883° W). We identified study sites using the greenspace database (<http://digimap.edina.ac.uk/os>), specifically, we selected all areas classified as public greenspaces (i.e. public parks, playgrounds, golf courses, natural areas, etc.) within the city limits. In total, this included 329 unique sites, varying in size between 0.0002 km² and 1.684 km²; with an average site area of 0.135 ± 0.22 km². Of this set of greenspaces, we were able to survey 273 unique sites; as 56 sites (17%) were not accessible, had been re-purposed, or no longer existed. The total extent of the urban Edinburgh study area was 213.35Km², and the surveyed sites covered 16.7% of the total area (Figure 1).

We surveyed each site twice in 2017. The two sampling periods were chosen to capture differences in red fox life history i) the “Spring” season (25th January to 4th May 2017) coincided with the period between breeding and cub emergence from the den; ii) the “Autumn” season (1st August to 5th October 2017), captured cub weaning and preceded the dispersal of sub-adults (Hewson and Kolb, 1980; Harris, 1981b).. At each site for each sampling period, we surveyed the perimeter of the greenspace and recorded the presence of all fox scats (faecal samples). Morphological identification of the scats was based on content (e.g. whether it contained bone fragments, hair or feathers), shape, size and colour (Heinemeyer *et al.*, 2008). For each scat, we recorded GPS coordinates and if was freshly deposited (i.e. not mouldy and still dark in colour) the sample was collected, weighted and stored in 10% buffered formalin solution at 4°C for further analysis.

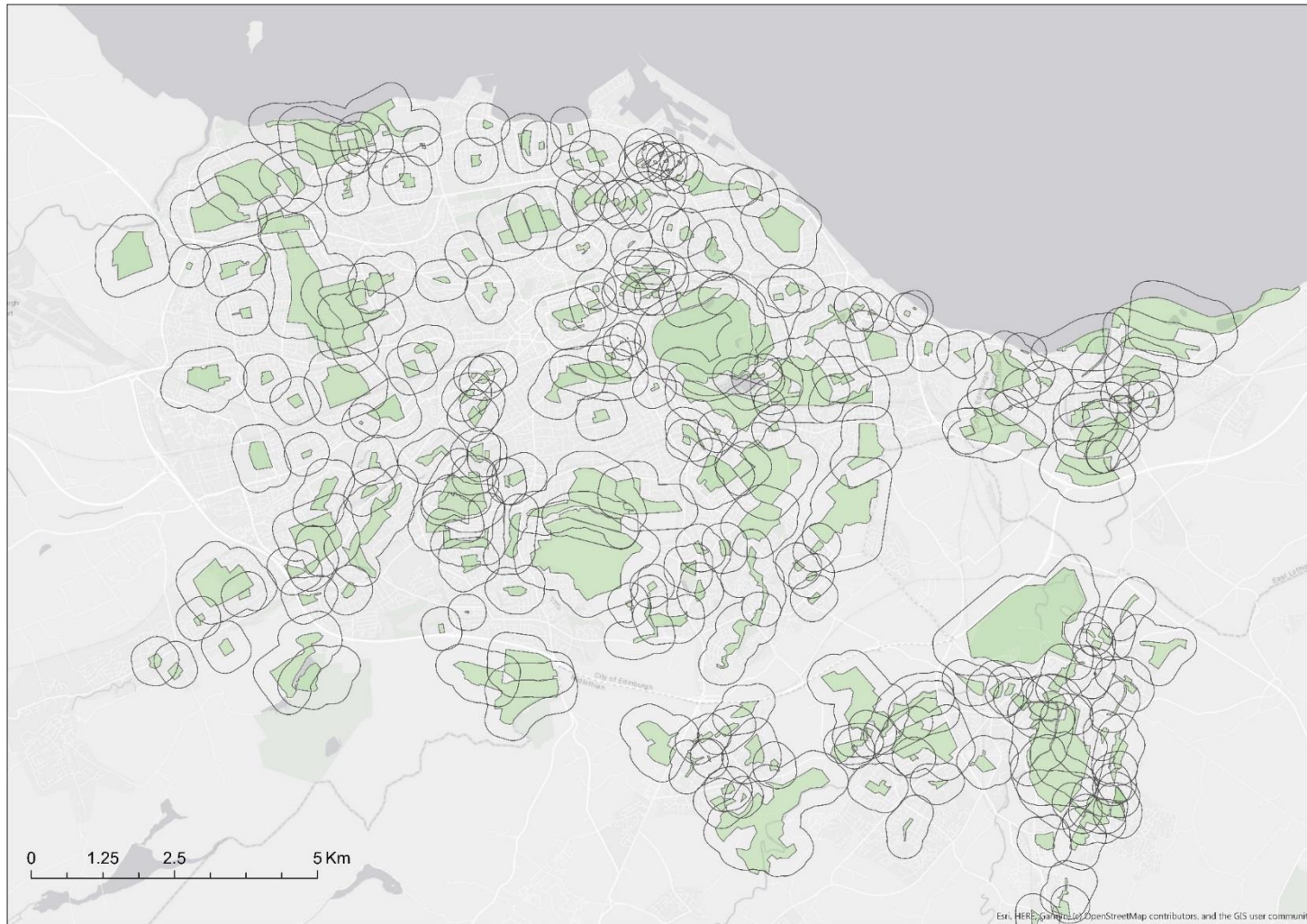


Figure 1 – Map of Edinburgh detailing the 273 greenspace survey sites (in green) with a 300m planar radius buffer used to calculate the urbanity measures. All sites were sampled during both of the two sampling periods (Spring and Autumn) in 2017.

Socio-economic and ecological variables

In order to effectively capture fine scale variation in the urban landscape, we measured both socio-economic and ecological variables. First we identified several socio-economic variables that reflect aspects of anthropogenic disturbance that are typically representative of urbanity (Hahs & McDonnell, 2006): human population density, road cover and traffic counts, and the ratio and variability of greenspace (Figure 2). We collated data for each site from publicly available databases:

- I) Resident human population density (<http://www.scotlandscensus.gov.uk>) is widely used as a proxy for urbanity and broadly reflects human abundance and land use (du Toit & Cillier, 2011).
- II) Road cover (<http://digimap.edina.ac.uk/os>) and traffic counts (<http://www.dft.gov.uk/traffic-counts>). Roads can act as barriers to dispersal (Magle *et al.*, 2009), by altering the geophysical characteristics of the environment (Yuan & Bauer, 2007; Gaston *et al.*, 2010) and their distribution correlates with habitat disturbance (Arnold & Gibbons, 1996). Traffic is the leading cause of fox mortality in cities (Gosselink, Van Deelen, Warner, & Mankin, 2007) which can generate marked changes in the demographic structure of urban fox populations (Baker, Dowding, Molony, White, & Harris, 2007).
- III) Greenspace ratio and variability (<http://digimap.edina.ac.uk/os>). Greenspaces are the most important urban areas as they provide suitable sites for wildlife to rest and breed. Greenspaces are defined as urban green areas such as parks and sports facilities, where building is limited or absent and where some form of vegetation is the primary land cover; (Taylor & Hochuli, 2017). Greenspaces are vital for urban foxes (Baker *et al.*, 2007), which are primarily active during the night and require safe hiding spots to rest during the day (Harris & Baker, 2001). In particular, areas of continuous suitable habitat play an important role in the connectivity of the urban landscape and can allow foxes to move around the urban areas relatively undisturbed (Schiller & Horn, 1997).

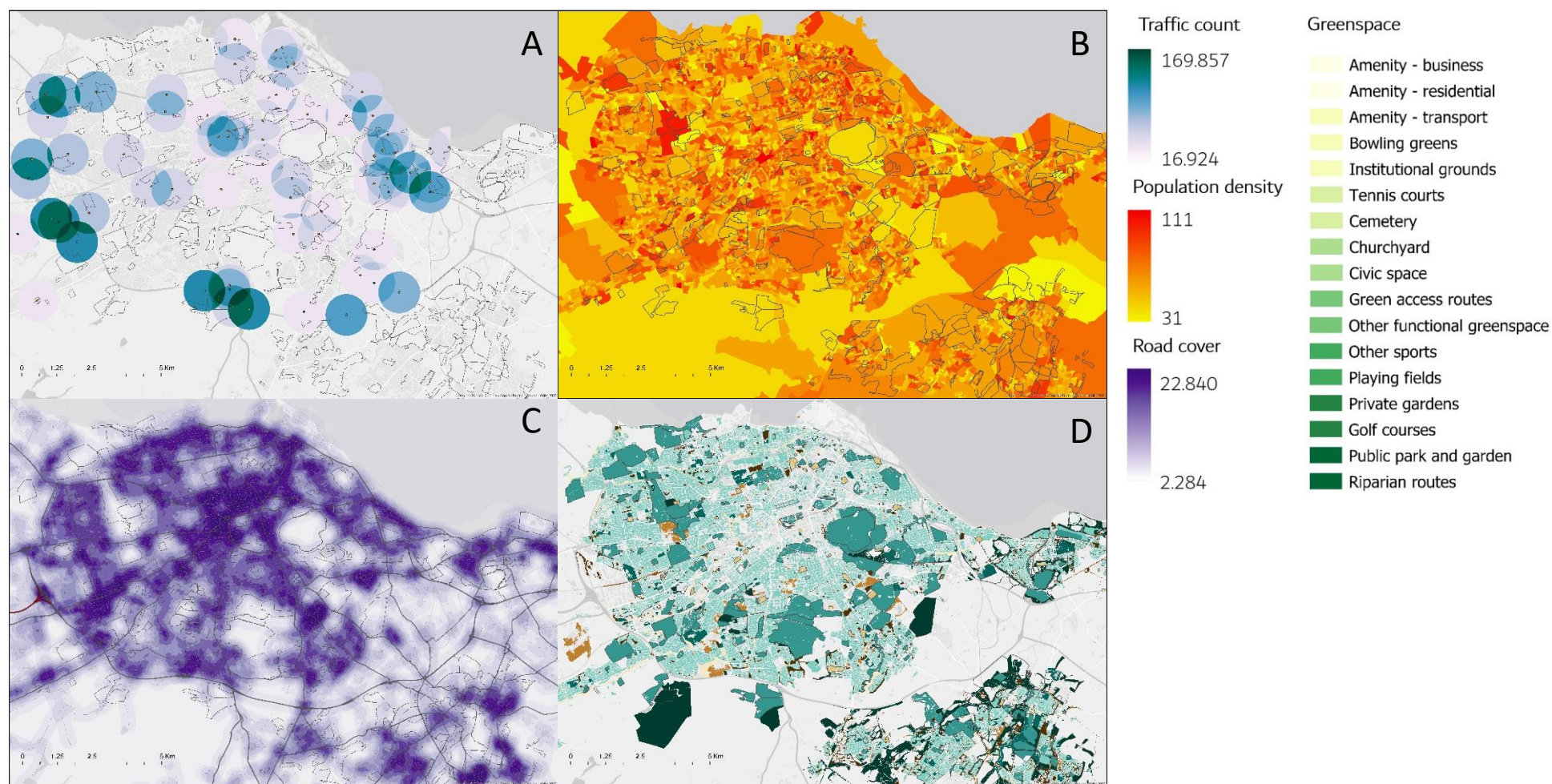
175 We also recorded the following four ecological variables that describe important aspects of the biotic
176 habitat for each greenspace site surveyed:

- 177 I) Presence/absence of European rabbits (*Oryctolagus cuniculus*). These medium-sized (2-4kg)
178 lagomorphs are one of the main prey species of red foxes (Lees & Bell, 2008) and are present
179 across Edinburgh.
- 180 II) Presence/absence of roe deer (*Capreolus capreolus*). The presence of large ungulates, such as
181 roe deer, while not directly related to fox diet as they are too large to be prey, serve as a
182 useful proxy indicator for the overall 'wilderness' of a site (Magle *et al.*, 2014).
- 183 III) Presence/absence of European gorse (*Ulex europaeus*). The vegetation of this plant, which is
184 found across both urban and rural habitats across the UK, is particularly impenetrable. It can
185 create secure, suitable microhabitats within human-dominated or disturbed greenspaces
186 where foxes, and other urban wildlife, may safely rest and breed (White, Gubiani, Smallman,
187 Snell, & Morton, 2006).
- 188 IV) Vegetation management regime. Management of greenspaces can vary from high intensity
189 amenity grassland to very low intensity semi-natural woodland or moorland, with likely
190 consequences for prey abundance and diversity (Goddard *et al.*, 2010), the availability of
191 resting and denning sites, and the extent of human incursion and disturbance. We assessed
192 this index as the intensity of the management rather than its extent, on a scale from 0 (the
193 site vegetation was left completely untouched), to 4 (large portions of the site were actively
194 managed throughout the year; e.g. by cutting the grass).

195 Each socio-economic variable defined above was mapped across the entire study area using a
196 25mx25m raster ArcGIS pro 1.4 (ESRI, 2017). We extracted the average value relative to each site
197 using the zonal statistics tool. For the greenspace variability metric, we obtained both the average
198 greenspace cover (i.e. ratio of green area/total area) and the variability of greenspace, which is

expressed as the number of different greenspace categories (out of the 25 identified by remote sensing in the dataset).

Given previous estimates of urban fox home ranges ($\sim 1.75\text{Km}^2$ for resident adults; Castañeda *et al.*, 2019), it is likely that foxes living in a specific greenspace will roam to neighbouring areas and could be affected by the level of urbanity beyond the specific sites where scats were found. To account for this, we extracted the values for each socio-economic variable from the surrounding areas, by including a buffer polygon with a radius of 300 planar metres around each site, which was chosen to reflect the reported average distance travelled by foxes in non-dispersing movements (Iossa *et al.*, 2008). Each buffer area included landscape features that were most likely to represent the habitual home range of the foxes living in each site. All socio-economic variables were continuous but measured in different scales, thus we standardised each to a mean of zero and variance 1 to avoid convergence problems in the models.



Gastrointestinal (GI) parasite community

All fresh fox faecal samples were analysed using salt flotation and microscopy in order to identify parasite species and abundance, based on egg/oocyst morphology using a Veterinary Parasitology key (Foreyt, 2001). When possible, we identified each parasite to species level, however in some cases this was not possible and so we identified each parasite to the lowest taxonomic level possible. For each fox faecal sample, we recorded: (i) presence/absence (0/1) and (ii) burden (eggs/oocysts per grams) for each parasite taxon, (iii) species richness (number of GI parasite species/taxon) and the (iv) Shannon diversity index. Specifically, the Shannon diversity index (H) was calculated using the package *vegan* (Oksanen *et al.*, 2015). This is a metric commonly used to evaluate the diversity of an assemblage, taking into account both relative abundance and species richness (Chao *et al.*, 2014).

Statistical analysis

To determine if there was a pattern in the distribution of red fox scats found across greenspaces in urban Edinburgh, we fit a generalised linear mixed model (GLMM) with the socio-economic and ecological variables (details below) as predictors of red fox marking (number of scats found per site). Next, we fit a series of GLMMs to determine the impact of urbanity on the fox parasite community. Specifically, we tested the effect of the socio-economic and ecological variables on: (i) overall parasite infection risk (presence/absence of each parasite species), (ii) parasite species richness and (iii) parasite community composition (Shannon diversity index). Finally, we fit individual models to test the effect of these variables on single parasite species infection risk (presence/absence) and burden (eggs/oocyst per gram).

We also tested for spatial autocorrelation in the dataset using a variogram of the Pearson's residuals from each model (fitted without a spatial term). All models showed evidence of spatial autocorrelation, and so we included a spatial term using a conditional autoregressive correlation model with a Matérn correlation structure in each model (Rousset & Ferdy, 2014) using the package

spaMM (Rousset *et al.*, 2018). All models were fit using the function HLfit (adjusted by maximum likelihood) and the fixed effects were tested for significance using the function fixed LRT.

Before fitting each model, we also checked for collinearity between the variables by calculating the variance inflation factor, which provides an index measuring how much the variance of the estimated regression coefficient is increased because of collinearity. we used a value of 2 as cutoff for exclusion (following Craney & Surles, 2002), which revealed that some of the ecological variables which were fit as factors (specifically the presence/absence of rabbits, roe deer and gorse) were significantly correlated. Therefore we combined these three ecological metrics into a single composite variable called “urban wilderness” which had three levels (“0”, “1” and “2 or 3”), representing the number of these three possible species recorded at each site.

Each model included the following fixed effects measured at each site (inclusive of the 300m buffer around each greenspace): five socio-economic variables (population density, road cover, traffic counts, greenspace ratio and variability) and two ecological variables (urban wilderness and the level of vegetation management). We also included the sampling period as a factor (Spring and Autumn), site area (m²; log transformed), and site transect length (m) as an offset to account for the different transect lengths in each site. The first model which tested how these variables impacted the number of scats found per site was fit using a Poisson distribution and included Site ID and a Matérn spatial correlation structure as random effects. To investigate the drivers of parasite species richness (count data) and the Shannon diversity index (H; continuous) we fit Poisson and gaussian distributions respectively, and included Sample ID (species richness only), Site ID and Matérn spatial correlation structure as random effects. Finally, the model fit to evaluate the likelihood of infection with all gastrointestinal parasite taxa (measured as presence/absence per parasite taxon per sample), was fit using a Bernoulli distribution and included parasite taxon identity as a fixed effect and Sample ID, Site ID and Matérn spatial correlation structure as random effects. The species-specific models included a

binomial (Bernoulli) distribution model fit on parasite prevalence (presence-absence of each parasite taxon per sample) and a Poissons distribution model fit on burden data (eggs/oocysts per gram).

Results

Red fox scat distribution across urban Edinburgh

We sampled 237 greenspace sites across the urban environment of Edinburgh during two sampling periods in 2017, we found a total of 287 fox scats: 144 in Spring and 143 in Autumn. Overall 224 (78%) were collected for gastrointestinal parasite analysis: 118 and 106, respectively in Spring and Autumn. Red fox scats were found only in 50 of the greenspace sites (18.3%), and this pattern was consistent

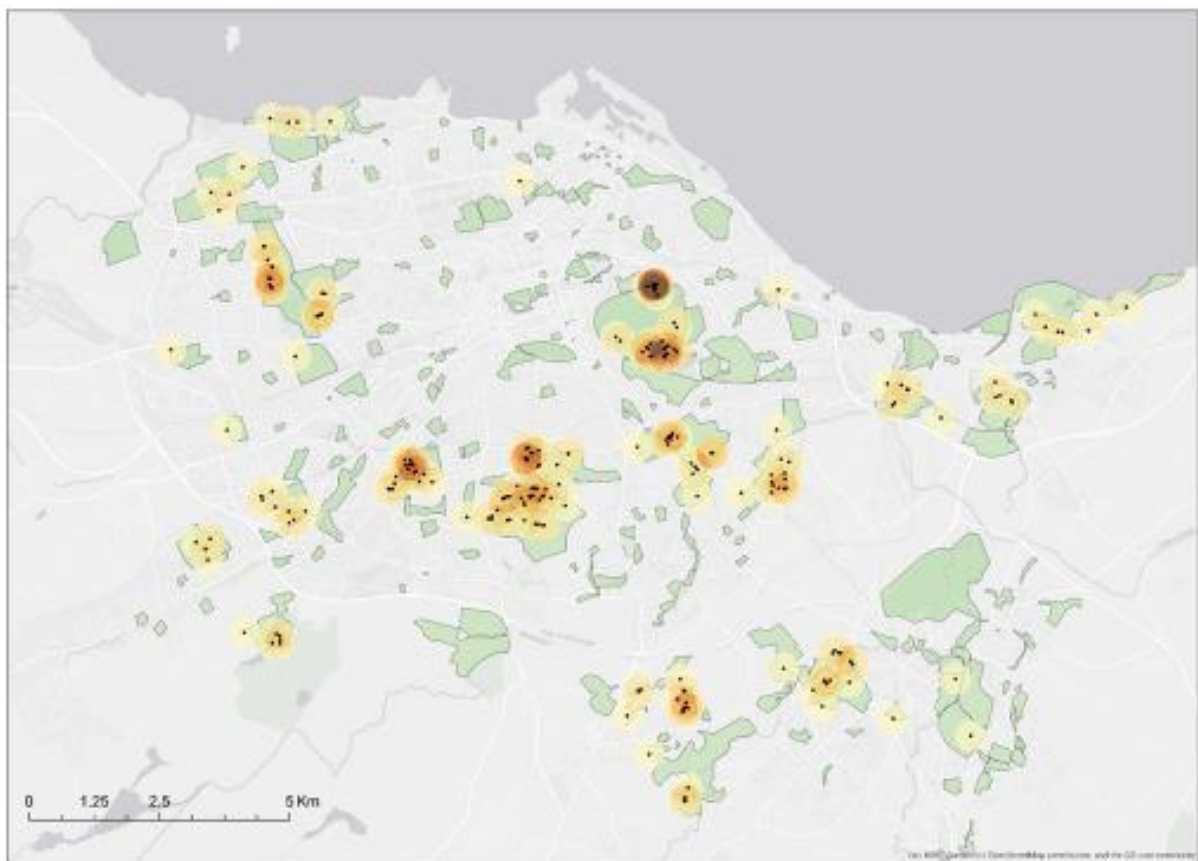


Figure 3 - Map of the study area (urban Edinburgh), highlighting all the survey sites in green ($n=273$; 16.7% of the entire map area). All Red fox scats that were found across both seasons are represented by black dots. The density of scats across the area is mapped using a kernel density function with a radius of 300m. The colour represents the number of scats found per square metre from dark orange to transparent ($\text{min}=0.00024$, $\text{max}=0.0255$).

across both seasons (35 sites in the spring, 36 in the autumn of which 21 had scats in both seasons).

Furthermore the average number of scats per marked site were 4.04 ± 2.40 (Range = 1- 27; Spring =

4.11 ± 3.82; Autumn = 3.97 ± 5.24), indicating that if a site was marked, it was likely to contain multiple scats.

Fixed effects	Estimate	SE	t-value	p-value
<i>Intercept</i>	-12.029	1.885	-6.381	
<i>Road Cover</i>	0.041	0.222	0.182	
<i>Traffic counts</i>	-0.017	0.149	-0.118	
<i>Population Density</i>	-0.028	0.162	-0.174	
<i>Greenspace Ratio</i>	2.374	0.971	2.443	*
<i>Greenspace Variability</i>	0.021	0.0259	0.821	
<i>Sampling period (Autumn)</i>	-0.373	0.212	-1.755	
<i>Site Area (Log)</i>	0.052	0.159	0.329	
<i>Urban Wilderness (1)</i>	2.050	0.506	4.044	***
<i>Urban Wilderness (2-3)</i>	3.166	0.510	6.200	***
<i>Veg Management level (1-2)</i>	-0.090	0.478	-0.189	
<i>Veg Management level (3-4)</i>	-0.570	0.433	-1.316	
Random effects	Variance			
<i>Site ID</i>	0.392			
<i>Spatial effect</i>	0.355			

Importantly, we found the number of fox scats found at a site was determined by both socio-

*Table 1 – The output for the model fit to determine which factors influence the number of scats found in each greenspace across urban Edinburgh. The variables included in the models are listed with model estimates, standard error (SE) and t-values. The p-values were calculated using a likelihood ratio test using the fixedLRT function in SpaMM. * p < 0.005, ** p < 0.001, *** p < 0.0001.*

economic and ecological factors. Specifically both the greenspace ratio (t = 2.4432, p = 0.0233) and the composite ‘urban wildness’ score (t = 4.0447 and t = 6.2009 respectively for the two levels, p < 0.0001; Table 1) were significantly and positively associated with a higher number of scats found.

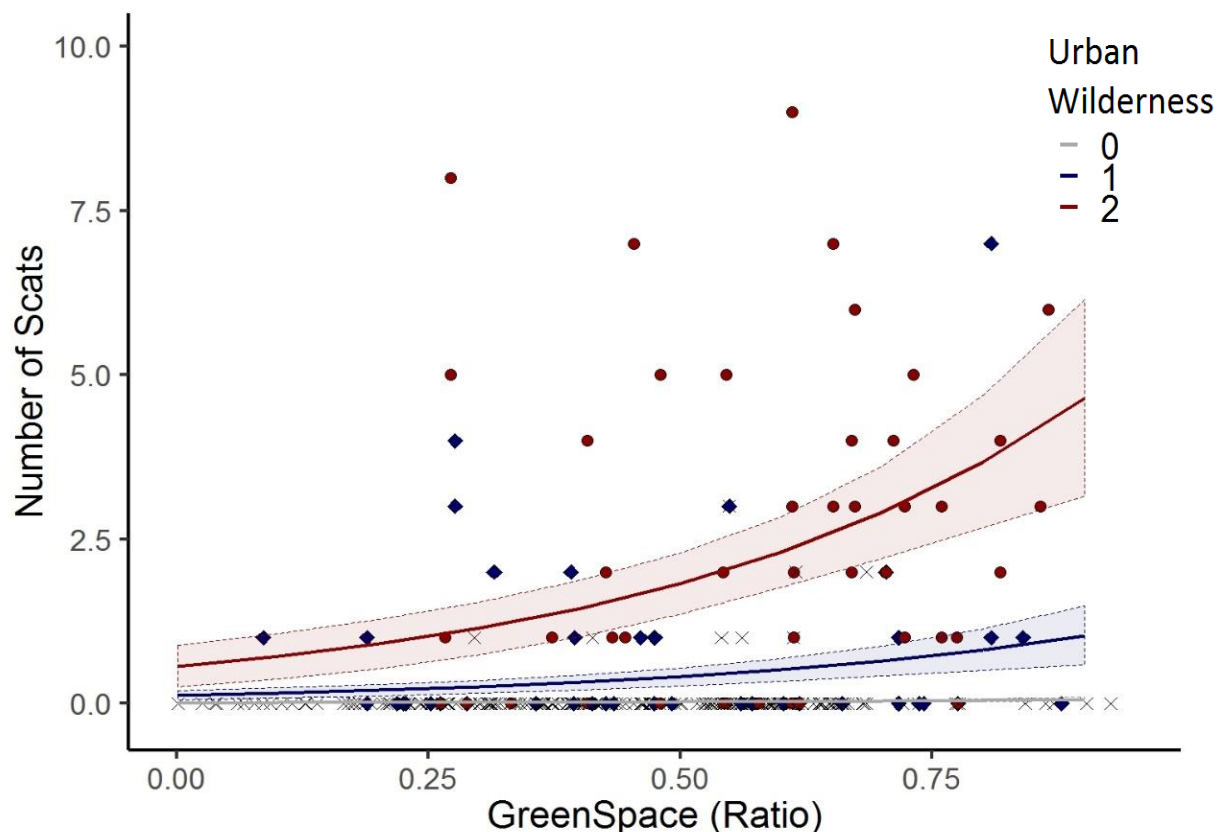


Figure 4 - Model prediction from the GLMM on number of Red fox scats found per site. Greenspace ratio was positively associated with the number of scats found, we also found a positive relationship with 'urban wildness' score, with a higher number of fox scats found in sites where we record the presence of other species (roe deer, rabbits and gorse). The grey line represents greenspaces with no wild species found, the blue line represents sites with one species and the red one sites with two or three species recorded. The raw data is also included in the figure as specific points, in the same colour scheme.

Gastrointestinal parasite community

We identified six parasite taxa from the fox faecal samples collected across Edinburgh.

Specifically, we found four helminth taxa, including three nematodes and one cestode, and two species of coccidian parasites. Due to limitations with taxonomic resolution for parasite identification, we were able to identify three parasitic helminths to species level: *Toxocara canis*, *Eucoleus aerophilus* and *Uncinaria stenocephala*, while the other three taxa were identified to genus level (helminth: *Taenia* spp. and coccidia: *Eimeria* spp. and *Isospora* spp.).

Overall, 83.9% (118 out of 224) of the faecal samples contained helminth eggs or coccidian oocysts of at least one parasite taxon, and parasite infection (defined as infection with at least one taxon), was slightly higher in the spring (87.3%) than autumn (79.4%). There was also variation in the overall

prevalence of each parasite taxon found, with helminth parasites being more common (79% of samples had at least one taxon) than coccidia. (45.9%; Table 2). The prevalence of different parasite taxa varied considerably, with only 8.9% of the samples found to contain *Taenia spp.*, while 45% were positive for *U. stenocephala*. The average parasite species/taxon richness per sample was 1.96 ± 1.34 (Spring = 2.18 ± 1.31 ; Autumn = 1.72 ± 1.32 ; Table 2).

Taxon	Summer		Autumn	
	Prevalence	Burden	Prevalence	Burden
<i>Eimeria spp.</i>	42.8	24.59	30.8	199.53
<i>Isospora spp.</i>	10.1	0.24	17.7	2.08
Total Coccidia	47.0	24.82	43.0	201.61
<i>Euculeus aerophilus</i>	52.1	1.08	32.7	3.13
<i>Toxocara canis</i>	14.3	2.68	13.1	14.41
<i>Uncinaria stenocephala</i>	47.1	4.59	42.0	4.70
<i>Taenia spp.</i>	12.6	1.10	4.67	0.12
Total Helminth	82.3	11.32	72.9	11.82

Table 2 - Parasite prevalence (%) and average burden (average eggs/oocysts per gram of faeces, measured across all samples) for GI parasites of Red fox scat samples collected across greenspaces in urban Edinburgh in 2017, for each of the two survey seasons: Spring (January to April), and Autumn (August to October).

We found that the models fit to evaluate the effect of urbanisation on the three broad GI parasite metrics (overall probability of infection, species richness and parasite Shannon diversity) were qualitatively similar (Table 3 and 4). All three analyses, demonstrated a positive association between the parasite metric and greenspace ratio ($t=2.679$, $p=0.007$, $t=2.881$, $p=0.008$, and $t = 3.238$, $p = 0.001$ for infection probability, SR and H index respectively); while the second sampling period was negatively associated with three metrics ($t=-2.419$, $p=0.0215$, $t=-2.500$, $p=0.022$, and $t=-2.350$, $p = 0.026$ for infection probability, SR and H index respectively). Additionally, the Shannon diversity index of parasite diversity was found to be positively associated with both greenspace variability ($t =2.277$, $p = 0.0246$) and traffic counts ($t =1.994$, $p = 0.0487$).

Fixed effects	Estimate	SE	t-value	p-value
<i>Euculeus aerophilus</i>	1.246	2.296	0.542	
<i>Taenia spp</i>	-1.035	2.305	-0.449	
<i>Toxocara canis</i>	-0.508	2.300	-0.221	
<i>Uncinaria stenocephala</i>	1.330	2.296	0.579	
Coccidian parasite	1.351	2.296	0.588	
Road Cover	0.117	0.138	0.851	
Traffic counts	1.477	0.162	0.109	
Population Density	0.030	0.115	0.262	
Greenspace Ratio	2.671	0.996	2.679	**
Greenspace Variability	0.061	0.039	1.566	
Sampling period (S2)	-0.478	0.198	-2.419	*
Urban Wilderness (1)	-0.006	0.524	-0.012	
Urban Wilderness (2-3)	0.187	0.433	0.432	
Site Area (Log)	-0.395	0.277	-1.424	
Veg. Management level (1-2)	-0.274	0.437	-0.627	
Veg. Management level (3-4)	-0.678	0.374	-1.811	
Random effects	Variance			
Site ID	5.837e ⁻⁰⁹			
Sample ID	0.1629			
Spatial effect	0.3812			

Table 3 – GLMM output of the Bernoulli model for the likelihood of gastrointestinal parasite species/taxa infection (presence-absence). The variables included in the models are listed on the left, along with estimate, SE and t-values. The p-values for each fixed effect were computed applying a likelihood ratio test. * $p < 0.005$, ** $p < 0.001$, *** $p < 0.0001$

The species-specific models for the helminth parasite species included individual models fit for *E. aerophilus* and *U. stenocephala* prevalence and burden, *T. canis* prevalence. The models fit to *T. canis* and *Taenia spp* did not converge; likely due to lack of data. Given the difficulty in identifying coccidian protozoans to the species level, we ran models evaluating the overall coccidian prevalence and burden (inclusive of both taxon). The models did not show any overall trend (see supplementary material for the full output of the models). We found that greenspace was positively correlated with *U. stenocephala* prevalence and burden ($t=2.037$ and $t=2.238$); *E. aerophilus* was less prevalent and less abundant in the second survey season ($t=-3.199$ and $t=-4.177$) and both *E. aerophilus* and the

341 coccidian parasites prevalence was significantly correlated with the level of urban wilderness, but in
342 opposite direction ($t = -1.616$ and $t = 1.835$ respectively). None of the variables included in the model
343 had a significant effect on the prevalence of *T. canis*.

Fixed effects	Species richness (SR)				Shannon diversity index (H)			
	Estimate	SE	t-value	p-value	Estimate	SE	t-value	p-value
<i>Intercept</i>	0.331	1.274	0.259		0.033	0.572	0.059	
<i>Road Cover</i>	0.066	0.073	0.906		0.043	0.033	1.298	
<i>Traffic counts</i>	0.047	0.054	0.879		0.053	0.027	1.994	*
<i>Population Density</i>	0.049	0.057	0.859		0.009	0.027	0.311	
<i>Greenspace Ratio</i>	1.511	0.524	2.881	**	0.779	0.238	3.268	**
<i>Greenspace Variability</i>	0.022	0.020	1.075		0.021	0.009	2.277	*
<i>Sampling period (Autumn)</i>	-0.263	0.105	-2.500	*	-0.118	0.05	-2.35	*
<i>Site Area (Log)</i>	0.189	0.302	0.627		-0.022	0.134	-0.169	
<i>Urban Wilderness (1)</i>	0.208	0.249	0.837		0.005	0.112	0.044	
<i>Urban Wilderness (2-3)</i>	-0.078	0.151	-0.515		-0.03	0.069	-0.42	
<i>Managed Vegetation level (1-2)</i>	-0.253	0.232	-1.090		-0.11	0.108	-1.012	
<i>Managed Vegetation level (3-4)</i>	-0.417	0.188	-2.209		-0.159	0.092	-1.719	
Random effects	Variance				Variance			
<i>Site ID</i>	6.58 e ⁻⁰⁹				4.67 e ⁻⁰⁹			
<i>Spatial effect</i>	9.55 e ⁻⁰⁶				6.43 e ⁻⁰⁹			
<i>Sample</i>					7.64 e ⁻⁰⁹			

Table 4 – The GLMM model output for the GI parasite diversity (Shannon Index) and species richness models. The variables included in the models are listed on the left, along with estimate, SE and t-values. The variance explained by the random effects are also included at the bottom.

The p-values for each fixed effect were computed applying a likelihood ratio test using the fixedLRT function in SpaMM. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Discussion

Using a comprehensive, repeated survey of greenspaces throughout the urban landscape of Edinburgh, we found evidence that fine-scale landscape variation plays important roles in determining both red fox marking patterns and their gastrointestinal parasite infection community. Specifically, we found that the amount of greenspace in and around each site (300 meter buffer) was positively associated with the number of fox scats found in a site (an indication of fox territorial marking) and GI parasite diversity, species richness and likelihood of infection. Areas with a higher greenspace ratios contained more red fox scats, and in addition these faecal samples were more likely to be infected with GI parasites, as well as having more diverse parasite communities.

Red fox scats had a distinct, highly localised, distribution across Edinburgh and the strongest predictor for the number of scats found was the composite measure “urban wilderness”. This ecological metric included the number of other wildlife and plants species (specifically rabbits, gorse, and roe deer) present in a site. Specifically, sites that supported other wildlife/plants tended to be more heavily marked by red foxes, while sites with no or few of these species had far fewer red fox scats. In wild, non-urban habitats, red foxes have been shown to mark uniformly throughout their territory (Macdonald, 1980) and accordingly, we hypothesised that all the sites visited by foxes should be equally marked. However, our results suggest otherwise, and a clear pattern of marking emerged from our survey.

Most of the marked sites were considerably smaller than the reported size of urban fox home ranges (0.115 - 0.458 Km²; Marks & Bloomfield, 2006) and therefore it is unlikely that neighbouring greenspaces would not be visited by resident foxes. Moreover, in a previous study of red fox movement conducted in the city of Edinburgh, Kolb (1985) reported extensive use of some habitat types that we found completely unmarked (e.g. cemeteries). In addition, our personal observational data supports the hypothesis that red foxes can be found roaming and foraging on unmarked sites at night across Edinburgh (Gecchele *et al*, unpub data). We suggest that a possible hypothesis for the

observed non-uniform scat distribution patterns found across the urban landscape of Edinburgh is that scat marking is most concentrated in the core area of a foxes' territories, while surrounding greenspace areas may be visited for foraging purposes, but are left unmarked. Greenspaces that host other wild species are more natural-like and are more likely to provide suitable resting and denning sites; the higher number of scats found in these areas could be a result of higher territorial marking driven by competition for territories in these areas.

The ratio of greenspace within and around each site was the single most important predictor of GI parasite infection risk, species richness and diversity, being positively correlated with all three metrics. Scats collected in sites surrounded by a higher amount of greenspaces were more likely to be infected with at least one parasite species, and had a larger and more diverse parasite community. This metric of 'greenspace ratio' can be considered a measure of landscape connectivity, since urban carnivores tend to use green areas to move around urban landscapes (Dodge & Kashian, 2013). As such, larger greenspace ratio scores suggest more contiguous greenspaces, which gives red foxes a chance to move safely across the urban environment (Kolb, 1984). At the same time, a higher concentrations of scats in the marked sites, may have important consequences for the transmission and infection burdens of gastrointestinal parasites of the foxes. Mathematical modelling have shown how increased marking rates can increase GI parasites prevalence (Nunn, Thrall, Leendertz, & Boesch, 2011), while studies in raccoons suggests that the clustering of individuals can increases the prevalence and species richness of GI parasites (Wright & Gompper, 2005). A recent study conducted on red foxes from Berlin focused on the effect of the urban landscape structure on seroprevalence of canine distemper virus (CDV) using fox carcasses collected around the city. Similarly to our results, they found that amount of greenspace in the area surrounding the carcass was positively correlated with the probability of seropositivity, but only for juvenile animals (Gras *et al.*, 2018). The authors concluded that access to more greenspace for juveniles was associated to a higher potential for dispersal and hence a higher risk of disease transmission. While we were not able to distinguish between individuals nor measure any demographic characteristics of the red foxes that deposited

each scat, our results also suggest a connection between the amount of greenspace and the prevalence and diversity of GI parasites. This overall effect of greenspace ratio on parasite prevalence and abundance was not reflected on the single-species models. These models did not show any broad trend, with several different variables having a significant effect on the prevalence and burden of different parasite species (including greenspace, sampling period and urban wilderness). This could be due to reduced statistical power, as the data for a single parasites will be more zero-inflated (in fact some models failed to converge).

Most previous studies of urban disease ecology have focused on how resource abundance and distribution in urban environment can affect host-parasite interactions (see for example Bradley & Altizer, 2006; Mackenstedt *et al.*, 2014). Here, we argue that we must move beyond a focus on resource availability, instead we should be measuring fine-scale variation in both socio-economic and ecological factors that can determine how the urban landscape can impact parasites and pathogens. For example, human density population has been shown to be positively correlated with the amount of anthropogenic food available to urban foxes in Zurich (Contesse *et al.*, 2004), but this variable was not significantly correlated with either the presence of red fox scats, nor the GI parasite prevalence and diversity in our study. Instead, we find that the amount of greenspace, and the presence of other 'wild' species may be better indicators of how the habitat suitability varies across urban environments and may affect ecological interactions that lead to changes in the infection dynamics.

For logistic reasons we only surveyed public greenspaces and were not able to collect data on fox scat distribution or GI parasite infection from private gardens/greenspaces. Previous studies on urban foxes have shown that private gardens can represent an important source of anthropogenic food for red foxes (Contesse *et al.*, 2004), but the suitability of private urban gardens for resting and denning purposes has been debated. Saunders *et al* (1997) found that back gardens were amongst the most favoured habitat for day resting, while Newman et al. (2003) found that 86% of denning sites were located in back gardens. However, this dropped to 40% when population density crashed

421 following a mange outbreak suggested that private gardens may not be the most desired nesting
422 areas. Conversely, other studies of urban foxes found that back gardens, despite being the most used
423 habitat, were not a suitable habitat for natal dens (Duduś *et al* 2014). In addition, we lack direct
424 information regarding each fox that deposited the scats and were unable to distinguish between
425 individuals. However we assume that faecal marking from a site is likely to be from a single fox group,
426 given the territoriality of this species (Doncaster & Macdonald, 1991). Finally, as in every scat survey,
427 morphological identification of samples in the field is not completely reliable (Davison *et al.*, 2002) and
428 it is possible that some samples we assigned to red foxes were from domestic dogs. This is a
429 confounding factor we are aware of, but we deemed it relatively uninfluential in the overall analysis.

430 Our study highlights the complexity of the interaction between the urban environment, the
431 wildlife hosts that live in it, and their GI parasite community. Our results showed how measuring socio-
432 economic and ecological variables at a very fine-scale within an urban environment, helped identify
433 which variables may be affecting both the marking behaviour of foxes and driving higher GI parasite
434 diversity and prevalence. Importantly, we show that not all urban environments are the same, and
435 that including fine scale landscape characteristics in these kinds of studies is a vital step toward a
436 better understanding of the underlying mechanisms driving infection dynamics in urban
437 environments.

438

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442 **Conflict of Interest**

443 None declared.

444 **Author Contributions**

445 LVG lead the project, collected, and collated the data, performed the laboratory analysis, conducted
446 the statistical analysis, and the data visualisation and wrote the original draft. ABP and MB provided
447 equal supervising and advising support, both in project conceptualisation and data analysis, and
448 reviewed and edited the manuscript.

449 **Data availability statement**

450 The data presented in this study and the code used to conduct the analysis will be made available in
451 github upon acceptance of this manuscript.

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