Fox and the city

Understanding the influence of urban environment on the disease ecology of red foxes

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Declaration

I have composed all the chapters in this thesis, and all analysis presented in the thesis are my own work.
All the data presented in this thesis was collected by me with the following exceptions:

- The fox hair samples analysed in chapter 2 were provided by third parties, as specified in the chapter.
- The diet analysis data presented in chapter 4 were carried out by Hannah Romanowski as part of her honours final project in 2019, using samples I have collected.
- The data used in chapter 5 for the meta-analysis was collected in collaboration with several research groups as specified in the chapter itself.

This work has not been submitted for any other degree or professional qualification.

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Ai mi’ Babbo, e alla mi’ Nonna
e a tutte le persone che ho perso lungo la strada,
in questo mondo e in quell’altro

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Abstract

The “city fox phenomenon” is a relatively new one. The presence of established Red fox (*Vulpes vulpes*) populations in highly urbanised areas was first reported from London at the beginning of the 20th century; since then the number and frequency of these reports have multiplied and this is now consider a global trend. The causes of this phenomenon remain largely unknown, although it is speculated that that changes in the structure of the urban fabric (such as the expansion of low-to-medium density housing) have created new suitable habitats for foxes to colonise.

The presence of foxes in urban areas is especially relevant since they carry parasites and diseases that are responsible for some serious pathologies in humans (e.g. rabies, alveolar echinococcosis). Therefore, the effect of living in urban areas can have on the prevalence of zoonotic parasites in wild foxes has been extensively investigated. The results of these studies are contradictory, finding both increases and decreases in parasite prevalence, depending on the parasite species, study location or both. This is hardly surprising given the complexity of urban landscapes; even finding a comprehensive definition of what is urban has proven a difficult (and yet unsolved) challenge. It is therefore important to consider different aspects of urban areas and the effects they can have on the disease ecology of urban foxes (including both behavioural, physiological and epidemiological aspects).

With my thesis, I aim to deconstruct urban environment isolating measureable metrics that can be used to understand the effect of urbanisation on the parasite community of red foxes. I combine practical and theoretical approaches, using both field surveys, laboratory analysis and statistical modelling in order to understand what drives patterns of infection in a wild mammal living in a highly anthropogenic environment. In chapter 2, I tested the use of stable isotopes analysis to detect and quantify anthropogenic food consumption between urban and rural foxes, as this has been linked to profound changes in the host-parasite dynamics in other urban carnivores. In chapters 3 and 4, I explored spatio-temporal dynamics in the gastrointestinal parasite community of urban foxes from the city of Edinburgh (UK). I used several metrics measuring different aspects of urban environment (i.e. human population density, road cover density and greenspace cover) to understand how the prevalence of these parasite vary across space (chapter3) and characterise longitudinal dynamics of infection (chapter4). Finally, in my fifth chapter, I use spatio-temporal hierarchical models to analyse a large dataset of fox infection data sourced from studies carried out across Europe, in order to characterise the overall effect of urbanity on parasite prevalence in foxes.

Altogether these findings contribute to the understanding of how urban environment influences the disease ecology of red foxes in particular and wild mammals in general; I developed tools to disentangle the complex and multi-layered effect of urban environment on the disease ecology of urban dwellers, contributing to the development of the field of both urban and disease ecology.

Lay Summary

The sight of a red fox in an urban area is becoming more and more common, especially in the UK, where this phenomenon was first identified in London in the early 1900s. In the past few decades, reports of foxes living in cities have multiplied, particularly from Western countries, such as Europe and North America. While the causes for this phenomenon are still uncertain, the consequences are well known; foxes are host to many parasites, some of which can be transmitted to people or domestic animals.

Efforts to eliminate fox populations by culling have been largely unsuccessful (and are now mostly been abandoned), and the focus of research shifted to try and understand the ways in which living in urban environment can influence the parasitology of foxes. Studies comparing the parasite prevalence (the % of foxes infected in a population) between urban and rural contexts are common; some have found a difference in the prevalence of certain parasites in urban areas, but the results are not consistent, even within research done on the same parasite species. A fact that is rarely taken into account is the fragmentation of urban landscapes and how vastly they vary in space and time, so much so that we still lack a proper comprehensive definition of what constitute an "urban environment". This has certainly contributed to hinder the quality of these studies and limit the generality of their findings.

In my thesis, I attempt to overcome these difficulties and define urban environments according to measureable characteristics, which can be measured in anywhere; I try to disentangle the complex relationship between these variables and understand which ones are important in determining the prevalence and strength of infection of gastrointestinal parasites in urban foxes from Edinburgh. I also use statistical modelling to try and identify large-scale patterns in the effect that urban environments can have on the probability of a fox to be infected by parasites. I use data from all over Europe, including both urban and rural fox populations, to determine whether there is a real effect of urbanisation.

With this work I hope to contribute to the understanding of the ways in which urban environment influences the life and parasitology of foxes.

Griffith did nothing wrong

Chapter 1

General introduction

Let's be perfectly clear, shall we?
The fox is not a little orange puppy dog
with doe eyes and a waggly tail.
It's a disease-ridden wolf with the morals of a psychopath
and the teeth of a great white shark.

Jeremy Clarkson (2005)

1.1 Rationale and Objectives of this thesis

The “city fox phenomenon” (Wandeler *et al.*, 2003)is a relatively new one; the presence of established Red fox (*vulpes vulpes*) populations in highly urbanised areas was first reported from London at the beginning of the 20th century (Teagle, 1967). Since then the number and frequency of these reports have multiplied and this is now consider a global trend; the causes of this phenomenon remain largely unknown, it is speculated that that changes in the structure of the urban fabric have created new suitable habitats for foxes to colonise (Harris, 1977).

The presence of foxes in urban areas is especially relevant since they carry parasites and diseases that are responsible for some serious pathologies in humans (e.g. rabies, alveolar echinococcosis; Gortázar *et al.*, 2007), therefore, the effect of living in urban areas can have on the prevalence of zoonotic parasites in wild foxes has been extensively investigated. The results of these studies are often contradictory, finding both increases and decreases in parasite prevalence, depending on the parasite species, study location or both (see for example Comte et al., 2013; Gras et al., 2018; Hofer et al., 2000; Reperant et al., 2007). This is hardly surprising given the complexity of urban landscapes; even finding a comprehensive definition of what is urban has proven a difficult (and yet unsolved) challenge (Weeks, 2010). It is therefore important to consider different aspects of urban areas and the effects they can have on the disease ecology of urban foxes (including both behavioural, physiological and epidemiological aspects).

With my thesis, I aim to deconstruct urban environment isolating measureable metrics that can be used to understand the effect of urbanisation on the parasite community of red foxes as well as identify overall patterns. I combine practical and theoretical approaches, using both field surveys, laboratory analysis and statistical modelling in order to understand what drives the patterns of infection in a wild mammal living in a highly anthropogenic environment.

1.2 Urban environments

The extent of urban areas are rapidly growing due to an ongoing urbanisation process. In 2008, the global urban population surpassed the rural one for the first time (United Nations, 2008). Cities are considered to be the apotheosis of un-natural environment and are built in response to the needs of people living in them, and constantly changing accordingly (Ramalho and Hobbs, 2012). However, there is a developing understanding that urban environments can host healthy ecosystems (Alberti, 2008; Galluzzi *et al*., 2010), although they can be very different from those found in natural environments (Francis and Chadwick, 2013). One of the most important characteristic of urban environment is that food availability is no longer a limiting factor for urban populations, anthropogenic food sources are generally abundant and not subjected to seasonal fluctuation (Shochat *et al*., 2006). At the same time, the scarcity of natural and green spaces and the fragmented nature of urban areas results in a scarcity of suitable resting and breeding sites (Franco *et al.*, 2005; Rubbo & Kiesecker, 2005; Scott Mills *et al.*, 1989). Anthropogenic disturbance is ubiquitous in cities and can affect wildlife in several ways; traffic (Etter *et al.*, 2002; Baker *et al.*, 2007), light (Longcore and Rich, 2004) and noise (Brumm, 2004) pollution can all negatively impact urban wildlife. Cities tend also to have a warmer, more stable micro climate than rural areas, due to abundances of impervious surfaces, general lack of vegetation and higher emission levels, a phenomenon known as “heat island” (Gaston *et al.*, 2010), which is subject to less seasonal fluctuations (Shochat *et al*., 2006).

Due to its unique characteristics, urbanisation can drastically alter the composition of wildlife communities; most species are incapable of adapting to live in urban environment and disappear altogether while other thrive and are capable of reaching much higher population densities than in natural settings (Evans, 2010). The lack of space is the de-facto limiting resource in urban areas and larger, more aggressive animals tend by absent from urban environments (Beckmann & Lackey, 2008; Hudenko *et al.*, 2010; Zorenko & Leontyeva, 2003). On the other hand, smaller, more flexible species can find in urban areas a favourable environment in which to live to live, thanks partially to absence of larger competitor species (Cypher and Frost, 1999) or lack of human persecution (Gloor *et al.*, 2001). Furthermore, cities are hotspots for the introduction of alien species that sometimes are only capable of surviving in the urban environment given its peculiar characteristics (Pickett *et al.*, 2001; Grimm *et al.*, 2008).

1.3 The role of parasites in ecological communities

Over the past thirty years, there has been a developing understanding of the role played by parasite in ecosystems (Hudson *et al.*, 2006); a growing body of research has investigated the complexity of parasite-mediated interactions and their influence on shaping ecological communities (Tompkins *et al.*, 2011).

The first level of influence (and the most obvious), is the effect that parasite infection has on individual hosts: the metabolic cost of fighting an infection can have in impact on growth (Sandland and Minchella, 2003), reproduction (Forbes, 1993), and survival (Moret and Schmid-Hempel, 2000) of the host. Often, the limited amount of resources available to allocate to metabolic functions also implies the existence of trade-offs between immune defence and other physiological processes (Hanssen, 2006; Schwanz, 2008).

Parasite infection can also have an effect at a population level; parasites can have a direct effect on host populations, reducing (Raffel *et al*., 2008) or even eradicating entire populations (McCallum, 2008) and some evidence indicates that parasites can have a role in amplifying naturally occurring oscillation in host populations (Forrester and Finley, 2006; Pedersen and Greives, 2008).

At a community level, parasites can influence the outcome of competitive interaction and predator-prey relationship (Hatcher *et al*., 2006). They can also play a role in biological invasions(Dunn *et al*., 2012; Prenter *et al*., 2004), as invasive species can carry parasites that have a greater effect on the resident, naïve hosts (Tompkins *et al*., 2003), ultimately resulting in a competitive advantage for the invasive species.

Finally, parasites can also have an influence on entire ecosystems; in recent years, the dramatic effect of parasite presence on food webs has started to be highlighted; parasites increase diversity and complexity of food webs (Dunne *et al.*, 2013), contributing to increase ecosystem resilience (Hudson *et al.*, 2006).

As the importance of these parasite-mediated processes becomes clearer, there is a developing understanding that studying host-parasite interactions in isolation in inadequate to properly understand the full effect that parasites have on ecosystems. For this reason, in recent years, much interest has been dedicated to understand these processes (Tompkins *et al*., 2011) which led to the development of the field of disease ecology (Hudson *et al.*, 2003).

1.4 Urban Disease ecology

Urban environment can have a direct effect on the ecology and behaviour of the species living there, but it also affect host-parasite dynamics and parasite communities. Several studies have established the profound effect that urban environment can have on parasite assemblages (Bradley and Altizer, 2006). Three key factors in particular have been shown to be particularly important in shaping host-parasite dynamics.

1.4.1 Resources

Resource availability is perhaps the most important factor in the ecology of urban species; abundant and stable sources of food impact urban dwellers both at individual (Cypher & Frost, 1999) and population levels (Riley *et al.*, 1998).

One of the most important effect of food availability in urban areas is the un-coupling predator-prey relationship: predation rate of carnivores in urban areas appear to be lower than in rural ones (Fischer *et al.*, 2012). Animals tend to be in better shape and hence be able to better fight off infections (Cypher & Frost, 1999). At the same time, food sources are not uniformly distributed, but highly clumped together, promoting a higher contact rate between individuals (Wright & Gompper, 2005), potentially resulting in a higher probability of infection for directly transmitted diseases (Devenish-Nelson *et al.*, 2014).

Furthermore, in natural environments, abundant but ephemeral sources of food can cause rapid growth and consequent crashes in populations (Ostfeld & Keesing, 2000); parasite can play a role in this cycle by exacerbating the process (Pedersen & Greives, 2008). However, urban areas tend to have abundant and stable food sources (Shochat *et al.*, 2006), that can prevent this kind of population crashes (Anderies *et al.*, 2007), reducing the impact of the parasites on population dynamics.

1.4.2 Micro-climatic conditions

The warmer, more stable micro-climate found in cities can have a direct effect on the distribution of some host species; urban migratory species can became resident (Bock and Lepthien, 1976), or new species can colonise cities that would not be included in their natural climatic range (Parris and Hazell, 2005). Changes in host ecological assemblages can reflect on the parasite community, with new parasites coming in contact with naïve host (Prenter *et al.*, 2004). The warmer urban environment can prove more suitable for vector species, leading to higher transmission risk in urban environment (Gibbs *et al.*, 2006; Rizzoli *et al.*, 2014). Urban micro-climatic conditions can also have a direct effect on parasites life cycles: many parasite species require a transmission stage (whether free-living or in a vector), that can be particularly susceptible to climatic conditions (Louis *et al.*, 2005). While a few studies exist investigating the role of climate in determining host-parasite assemblage on a worldwide scale (Brooks and Hoberg, 2007), data regarding the ways local micro-climatic conditions can affect free-living stages of parasites in urban areas are scarce.

1.4.3 Anthropogenic disturbance

Urban environment is characterised by high disturbance that can result in chronically high stress levels for wildlife. Glucocorticoid hormones produced in stress conditions can weaken the host immune system and intensify the effect of pathogens (Padgett & Glaser, 2003). Some studies have confirmed that population living in urban environment tend to have a higher level of glucocorticoids compared to rural ones (Ruiz *et al.*, 2002), but the negative effect of stress on host immune system has never been confirmed for urban wild populations. For example, an investigation on glucocorticoid levels conducted between rural and urban Kit foxes revealed chronically high basal levels of these hormones amongst urban population (Nelson, Creel and Cypher, 2015), even though a previous study on the same population found that urban foxes appeared to be in better physical condition and immunological tests revealed no differences between the two populations (Cypher and Frost, 1999). These factors have a differential effect on host and parasite species, sometimes with conflicting effects (Bradley & Altizer, 2006), creating a complex effect on host-parasite dynamics that is not easily explicable. For example, a milder climate can favour the survival of parasites in the environment, but the high availability of food sources can also reduce the impact of infection on the host given their better physical conditions. Furthermore different host or parasite species can have different responses to the same stimulus, depending on the ecological characteristics of the species; for example different parasite species can respond differently to food availability depending on their transmission mode (Reperant *et al.*, 2007a). In order to understand how urban environments affect host-parasite dynamics, I need to determine the effect of individual variables in the urban landscape in relationship to each of these factors and the effects that these three factors have on individual species.

1.5 Study system

1.5.1 Urban foxes

Wild carnivores are carrier of many parasites and are responsible for the transmission of many zoonotic diseases; livestock and domestic animals (Gortázar et al., 2007; Hassell et al., 2017) represent the first line of infection from wildlife and can pass diseases to humans. For this reason, the presence of wild carnivores in human-dominated landscapes is cause of concern for public health and one of the main reason for managing and culling efforts on carnivores in urban areas (Curtis and Hadidian, 2010a). Larger carnivores are less likely to be able to establish permanent populations in urban areas (McKinney, 2006; Bateman & Fleming, 2012) mainly due to conflict with humans and consequent persecution (Treves & Karanth, 2003). However, meso carnivores such as red foxes, Raccoons and Coyotes can potentially benefit from removal of top predators that in natural settings would suppress them (Ritchie & Johnson, 2009). Meso carnivores also tend to be more adaptable to new environment and more flexible in their food selection, adjusting well to alternative food sources and limited space (Crooks, 2002).

Arguably, the most successful mesocarnivores to adapt to life in urban environments is the Red fox (Vulpes vulpes); since the first record of the presence of foxes in London in the early 1900 (Teagle, 1967), this phenomenon has been observed worldwide (e.g Hofer et al., 2000; Uraguchi et al., 2008; Rosatte & Allan, 2009; Vuorisalo et al., 2014). The reasons for this are not completely clear, but there are speculation that changes in the structure of cities to include more green areas (both as private gardens and public parks; Harris & Rayner, 1986), or the end of large-scale epizootic outbreaks (e.g. rabies in Europe; Gloor et al., 2001) have contributed to this trend.

A relatively abundant literature exists covering various aspects of urban fox ecology, especially from the from the UK; this includes studies on population density, territory size and habitat preference (Baker et al., 2000; Newman et al., 2003), behavioural traits (Iossa et al., 2008; Whiteside et al., 2011), and recolonization after disease-induced local extinction, after an outbreak of Sarcoptic mange almost completely eradicated the Bristol urban fox population (Baker et al., 2000; Soulsbury et al., 2007).

In mainland Europe however, most of the research carried out on urban foxes have focused on the parasitology of this species and the effect that urban environment can have on host-parasite dynamics. This is probably due at least in part to the presence of several zoonotic pathogens such as rabies (Anderson et al., 1981) or, more recently, the Echinococcus multilocularis (Oksanen et al., 2016), which are absent from Great Britain.

Of particular importance are the helminth infections; foxes are the carriers of a multitude of GI parasites, most of which are shared with many domestic animals (both pets and livestock, Hassell et al., 2017).

1.5.2 Helminth parasites

A recent meta-analysis found that the red foxes is the mammalian species that host the highest number of zoonotic helminth parasites (Wells *et al.*, 2018); this is due to foxes global distribution (Soulsbury *et al.*, 2010) and adaptable behaviour (Fascione *et al.*, 2004), which makes them the come in contact with a vast array of parasites. Helminth parasites

(Nematoda, Cestoda, Trematoda, Acanthocephala) infections are extremely common in wild species (Taylor *et al.*, 2016), but they are rarely fatal and tend to be chronic conditions rather than acute. This is mainly due to the fact that helminth parasites, unlike microparasites, do not replicate within the body of the host and hence their number does not increase (and the infection becomes more serious), unless the host ingest another parasite of the same species (Anderson and May, 1991).

However, helminths can reproduce in the body of the host, producing eggs that are then shed through various means and that can then infect a new host. The life cycles of helminths are varied, but generally they all include a resistance form that can persist in the environment for long periods of time, either in the state of egg or larva; these are then picked up by a new host (either a definitive or an intermediate one), which will then become infected (Olsen, 1986).

These characteristics determine the demography of helminth parasitic infection; since they do not replicate in the host and it is unlikely that a host would pick up more than one (or few) eggs, the distribution of helminth infection among the hose population follows a typical negative binomial distribution, with the majority of infected individuals harbouring one or very few worms, while a few individuals would be very heavily infected (Brooker, 2010).

For this reason, in disease ecology helminth infections dynamics are generally characterised using a) prevalence (the proportion of individual infected) and b) the parasite burden which measures the number of parasite/parasite measurement metric per individual (Dobson & Roberts, 1995). In addition, in multi-species studies, the numbers of parasite species found in a host, or metrics of parasite diversity (such as Shannon or beta diversity) are used to characterise variation in the entire parasite community (Poulin, 1996, 1997).

The helminth parasite community of European foxes has been thoroughly investigated (See for example Thompson, 1976; Antolová *et al.*, 2004; Saeed & Kapel, 2006; Martínez-Carrasco *et al.*, 2007; Magi *et al.*, 2009; Miterpáková *et al.*, 2009; Franssen *et al.*, 2014). However, one parasite species in particular, the *Echinococcus multilocularis* has received more attention than any other.

1.5.3 Echinococcus multilocularis

The *Echinococcus multilocularis* is a tapeworm (Teniidae, Cestoda) with a distribution that extend to cover most of the norther hemisphere (Davidson *et al.*, 2012), but is considered highly endemic in Western and Central Europe (it is absent from the British isles; Davidson *et al.*, 2012). It is the etiological cause of the Human alveolar echinococcosis, which is considered to be one of the most serious zoonosis of the temperate zone (Torgerson *et al.*, 2010). The infection in humans generally happens as a result of accidental ingestion of contaminated soil; humans act as intermediate hosts for this parasite and can develop cysts in the liver caused by the larval stage of *E. multilocularis*. The condition can remain dormant for decades, but as the cysts grow, can cause damage of the liver and ultimately liver failure; it is a very serious pathology with a high mortality rate if left untreated (Kern *et al.*, 2003).

The progressive urbanisation of red foxes, main carrier of this parasite, sparked concerns for public health (Gloor *et al.*, 2001). As a consequence, many studies have been carried out specifically focusing on the link between urbanisation and the epidemiology of *E. multilocularis* (See for example Eckert & Deplazes, 1999; Contesse *et al.*, 2004; Hegglin *et al.*, 2007; Robardet *et al.*, 2008; Knapp *et al.*, 2018).

Deplazes et al. (2004) published a review of available data and formulated the hypothesis that predation on the intermediate host by foxes was reduced in urban areas due to the availability of anthropogenic food; as a consequence, the prevalence of *E. multilocularis* was lower in urban foxes compared to rural ones. However, it is important to note that results presented by Deplazes et al. were based almost exclusively on data from two urban populations from Swiss cities; other studies failed to replicate those findings, or achieved contrasting results, even between relatively close cities (Comte *et al.*, 2013, 2017).

1.5.4 Defining urban areas

Following up the review published by Deplazes et al. (2004), the same research group published another paper (Liccioli *et al.*, 2015), incorporating data from other studies from both Europe and Eastern Asia, highlighting how the kind of "urbes" can have different (sometimes contrasting) effects on the recorded prevalence of *E.multilocularis*.

This highlighted the need to take into account the heterogeneous nature of urban areas, both in space (each city has its own intrinsic characteristics, determined by cultural, historical and geophysical factors) and in time (cities are built to follow the need of their inhabitant and are constantly evolving; Cadenasso *et al.*, 2007). In addition, there are multiple variables of the urban landscape that have the potential to impact the ecology of wildlife (and have a cascading effect on their interaction with parasites), sometimes with different, and contrasting effects (Hahs & McDonnell, 2006). For example, while human population density is positively correlated with the amount of anthropogenic food available to urban foxes (Contesse *et al.*, 2004), it is also associated with the level of disturbance, making city centres a generally unsuitable environment for foxes (Wandeler *et al.*, 2003).

As a result, the urban-rural gradient does not follow a smooth transition between rural and urban, but each element follow a distinct spatial distribution, which can be related to others (e.g., traffic levels are dependent of road cover), but respond to different variables (e.g. road cover is highest in residential areas, where traffic is low; Forman & Hersperger, 1996).

All these factors contribute to make the study of the effect of urban areas on wildlife ecology a very complex subject. Furthermore, despite efforts to produce standardised measurement of urban variables, the available data is generally measured at country (sometimes region) level, which enhance the intrinsic heterogeneity of the data (Pumain *et al.*, 1991).

It is not for lack of trying that a comprehensive, objective definition of urbanity still does not exist (Pryor, 1968; Sayer, 1984; Isserman, 2005; Stewart *et al.*, 2007; Guérois and Pumain, 2008; Weeks, 2010; Zhang and Seto, 2011).

Given these caveats, it is not surprising that most studies focusing on the effect of urban environment on the disease ecology of urban foxes, simply report the results from areas that they consider to be representative of “urban” and “rural” (see for example Richards *et al.*, 1995; Fischer *et al.*, 2005; Reperant *et al.*, 2007b; Comte *et al.*, 2013). However this method of classification, while can be relevant and accurate for the specific system studied, is inherently subjective and does not allow for meaningful comparisons with other studies.

Given the complex structure of the urban landscape, and the difficulties associated with determining what urban environment even is, it is important to take into account the spatial element of the environment, and explicitly incorporate it in models fit to determine the effect of urban environment on the ecology of wildlife species.

1.5.5 Integrating spatial statistics in urban disease ecology

There are two main ways in which spatial statistics can contribute to the study of urban disease ecology in particular. The first way is involves incorporating spatially explicit measurement of relevant variables across the urban landscape; this has the distinct advantage of eliminating the need to determine the level of urbanisation of an area, which removes the subjective bias, since the variables are objectively measured across space (Mcdonnell & Hahs, 2013). For example, using the amount of greenspace available to the animal could provide a better metric of landscape fragmentation than a binary urban/rural classification (Gras *et al.*, 2018). Combining several metric allows to better account for the fine-scale variation in the urban environment and tease apart the effect of individual metric (Hahs & McDonnell, 2006). On a large scale this approach can find application in applying the same metric of urbanity, in a similar way that latitude is used as a proxy for temperature, even if at a local scale the microclimate of single locations depends on a multitude of factors (Poulin, 2004; Stephens *et al.*, 2016).

The second way is to explicitly incorporate spatial (and temporal) autocorrelation terms in the analysis of disease data; this approach corrects (to a certain extent) for any variable that might not have been taken into account, and causes localised unexpected variation (such as microclimatic conditions; Legendre, 1993). Until recently, applying spatio-temporal models to urban disease ecology research was unfeasible for most researchers (Blangiardo & Cameletti, 2015). Markov chain Monte Carlo (MCMC) based inference techniques have historically been the ones mostly used for spatial modelling (Besag & Green, 1993); however, this kind of inference is computationally expensive and not routinely used in disease ecology research. In the past decade however, a different Bayesian approach based on the integrated nested Laplace approximation (INLA) approach developed by Rue et al. (2009) has emerged as a computationally efficient alternative. INLA is designed to fit hierarchical models and to accommodate a spatio-temporal correlation term. The flexibility of this approach and the computational advantages it has in respect to other available methods, makes it a perfect candidate to evaluate the effect of urbanity on the disease ecology of urban wildlife.

These two methods are not mutually exclusive; indeed they complement each other, and I have applied them both in three of my chapters, trying to understand the fine-scale and overall effect of urbanity level on the disease ecology of foxes.

1.6 Thesis structure

The aim of the thesis is to characterise the effect of urban environment on the disease ecology of urban foxes. I present four data chapters aimed addressing different aspects of urbanity and to understand how they can influence host-parasite dynamics of urban foxes and their parasites, with a particular emphasis on gastrointestinal parasites.

Chapter 2 is a presents a preliminary analysis testing the effectiveness of stable isotopes analysis (SIA) to detect differences in the diet of rural and urban foxes with particular emphasis on anthropogenic food consumption. SIA has been used in the past to detect the amount of human-sourced food in urban carnivores in North-America, but has never been tested in Europe. Since anthropogenic food supply is one of the main characteristics of urban areas and can disrupt host-parasite dynamics in a variety of ways, this chapter represents a first introduction to the multifaceted effects that urban environment can have on the disease ecology of urban red foxes.

In chapter 3 I aim to deconstruct the environment of an urban area, accounting for fine-scale variation in the fabric of the landscape and understand how this variation can be important in influencing the disease ecology of urban foxes. I surveyed all the 273 public green areas in Edinburgh (UK) twice (in spring and autumn) and collected fox faecal marking along perimetral transects and used flotation analysis to identify gastrointestinal parasites. I then related several different socio-economic and ecological variables to the parasite prevalence and parasite diversity of scats found in each park. This chapter represent an in-depth look at how fine-scale variation in the urban landscape can influence the prevalence and diversity of parasites.

In chapter 4 I investigate temporal patterns in parasite prevalence, burden and diversity. I selected six sites within the Edinburgh urban areas and sampled them every three weeks between February and November 2018. I explore the effect of diet and microclimatic condition on the parasite community and try to statistically characterise these dynamics using different temporally explicit models to understand how the parasite community vary in time throughout the year.

In chapter 5 I attempt to detect overall patterns in the effect of urban environment on parasite and pathogens prevalence of red foxes. I collated a large georeferenced dataset comprising infection data from foxes collected by several different research groups from around Europe; I then characterised the parasite taxa according to functional traits and I constructed a large-scale, spatio-temporal model using R-INLA using remote sensing data of built-up space as a metric of urbanisation. I also fit a subset of the data to infer the effect of urbanisation on the prevalence of *E.multilocularis* specifically.

Finally, in chapter 6 I present a general discussion of my findings and examine the general implications of my results in the context of fox parasitology and disease ecology.

Chapter 2

Quantifying the amount of anthropogenic food in the diet of urban and rural red foxes using stable isotopes

This Fox has a longing for grapes:
He jumps, but the bunch still escapes.
So he goes away sour;
And, 'tis said, to this hour
Declares that he's no taste for grapes.

Walter Crane (1887)
The Fox and the Grapes

2.1 Abstract

The availability of anthropogenic food sources in urban areas is one of the main factors that can influence the ecology of urban carnivores, disrupting predator-prey relationships, competitive interactions and even having an effect on host-parasite dynamics. However, the detection of anthropogenic food in the diet is hard through traditional diet analysis. In recent years however, a technique based on the analysis of the stable isotopes ratio has emerged as a credible alternative to infer long-term, large-scale patterns in the diet of individuals and populations. The stable isotope analysis (SIA) rely on the structural differences in the isotope composition of different food sources, and has been successfully applied to urban carnivores in North America, where the presence of corn-based products in anthropogenic food shifted the Carbon isotope ratio of individuals consuming large quantity of this kind of food.

Here, I apply the same technique to red fox (Vulpes vulpes) hair samples from urban and rural areas, to assess the suitability of this technique in detecting the different diet composition of urban and rural foxes. My results showed no difference between the stable isotope ratio of urban and rural animals, suggesting that SIA is not a suitable technique for detecting consumption of anthropogenic food, at least in the context of opportunistically collected samples. However, given refinements this method could still be effective in detecting difference in fox diet. Further studies should take a more rigorous approach on sample collection by testing the hair of animals with known diet or known (distinctly urban/rural) territory.

2.2 Introduction

An increasing number of mammalian carnivore species have successfully adapted to living in urban settings (Randa and Yunger, 2006), where food sources are abundant, highly clumped and generally not subjected to seasonal fluctuation (Becker *et al.*, 2015). Urban areas can sustain populations of carnivores at much higher densities than natural settings (Bateman and Fleming, 2012), and the presence of carnivores in such close proximity to humans is generally problematic, as they tend to cause conflicts (Conover, 2002), but also because they can carry some parasites and pathogens species that can infect humans and/or domestic animals (Gortázar *et al.*, 2007; Mackenstedt *et al.,* 2014; Hassell *et al.*, 2017) Bateman & Fleming, 2012).

While it is clear that access to anthropogenic food, can impact wildlife populations, importantly it can also have both direct and indirect effects on dynamics of infectious disease (Becker *et al.*, 2015). For example, Murray, *et al.* (2015) found that urban coyotes in Edmonton (Alberta, Canada), were more likely to be malnourished and to be to be affected by mange, despite having access to more abundant and diverse amount of food; this was attributed by the poor quality of anthropogenic food the animals were consuming.

By contrast, Cypher & Frost (1999) found that urban kit foxes from Bakersfield (California, US) had access to more stable and abundant and stable food resources, and were in better conditions than rural foxes. There can also be indirect effects of anthropogenic food supplementation to wildlife, resulting in changes to intra-guild competition and predator-prey relationships. For example, a greater dependence on anthropogenic food can reduce predation on natural prey species that can serve as intermediate hosts for parasite species, which can, in turn, impact the host – parasite relationship (Fischer *et al.*, 2012). Abundant, localised sources of food found in many urban environments, such as landfill sites and rubbish bins, can also promote contact between individuals and species and contribute to the spread of directly transmitted diseases (Devenish-Nelson *et al.*, 2014).

It is therefore, important to be able to accurately detect the amount of anthropogenic food in the diet of urban carnivores, both to determine the implications for infectious disease, but also to address a number of ecological questions about carnivores including niche partitioning (Azevedo *et al.*, 2006), predator-prey dynamics (Weckel *et al.*, 2006),and even conflict management (Bagchi & Mishra, 2006). The most accurate method that is employed to determine the diet composition is through direct observation of animals while they forage in nature. However, this method is time intensive, unfeasible for many wildlife species, and unsustainable for large sample sizes and across long time periods. Therefore many indirect techniques have been developed and are currently being used to estimate the type and amount of food consumed by wild carnivores. Some of these methods are based on the visual identification of undigested remains in faecal samples (Ciucci *et al.*, 1996), or from stomach content, which are generally obtained in the context of culling programs (Hyslop, 1980); more recently molecular techniques have been used to identify food items from DNA (Symondson, 2002). While each technique can work for getting accurate measures of diet composition, they all also have limitations, for example, stomach content analysis involves culling animals, which is not feasible for the vast majority of studies, while the molecular identification of prey can be expensive.

Diet analysis of scats (the faecal marking of a carnivore) is arguably the most widely used method for wild carnivores (Klare *et al.*, 2011), but unfortunately also the most unreliable, both in terms of the identification of individual items (Gosselin *et al.*, 2017) and for estimating the relative volume of food groups in the diet (Balestrieri *et al.*, 2011). Furthermore, this kind of analysis only captures a “snapshot” of the diet of the animal, as only the remains of the previous (or few previous) meal can be detected.

Importantly, traditional diet analysis of carnivore scats generally fails to accurately estimate the amount of anthropogenic food in the diet; this is mainly because these analyses largely rely on the identification of undigested material, while anthropogenic food items tend to be completely digestible, and hence undetectable using these techniques (Fascione *et al.*, 2004). As a result, the amount of anthropogenic food in the diet of urban carnivores is probably routinely underestimated (Newsome *et al.*, 2010).

Recently, stable isotopes analysis (SIA) has become an increasingly popular tool to assess the diet of wild animals, and it is especially effective at capturing temporal (Dalerum and Angerbjörn, 2005) and spatial (Hobson, 1999) variations in diet. SIA detects variation in the ratio of the isotopes in a sample (animal tissue in this case) and can be used to detect the naturally occurring variation in this ratio from different food sources. For example plants with different photosynthetic pathways (such as C4) have a distinct $^{13}C/^{12}C$ ratio, while the ratio of $^{15}N/^{14}N$ increases with each trophic level in a food web, and can be used to evaluate the trophic niche of an animal (Gannes *et al.*, 1997). While this technique does not allow for the identification of single food items, it can capture overall trends in the diet, both in the short and longer term.

In the context of understanding the diet composition of wild carnivores, SIA has recently been used in North American studies to estimate the amount of anthropogenic food consumed by carnivores (Newsome *et al.*, 2010; Hopkins *et al.*, 2014; Murray, *et al.*, 2015), exploiting the fact that the North American diet tends to be rich in corn and corn-products (Chesson *et al.*, 2008; Jahren and Kraft, 2008). Consistently consuming this kind of anthropogenic food tends to increase the $^{13}C/^{12}C$ ratio of the animal tissue since corn is a C4 plant, preferentially fixing ^{13}C during photosynthesis compared to C3 plants. At the same time, the high prevalence of meat in the human diet means that the $^{15}N/^{14}N$ ratio is also higher, since ^{15}N is conserved more than ^{14}N through trophic levels (Gannes *et al.*, 1997). A few studies have successfully applied this technique to wildlife species in Europe, and found they a higher $\delta^{15}N$ in urban blue tits compared to rural birds, likely driven differences in the availability caterpillars (Pollock *et al.*, 2017),.

To date however, SIA has not been used to infer the diet of urban carnivores outside North America, because of the lack of a strongly corn-based human diet. Here, I tested whether SIA can be used to detect differential consumption of anthropogenic food in the diet of red foxes (Vulpes vulpes) from across the UK. I collected paired geographic samples from urban and rural settings, to test the assumption that urban foxes will have higher access and therefore consumption of anthropogenic food than rural foxes. I used the stable isotope ratio for Carbon, Nitrogen and Sulphur.

The results from this study could have deep implications for the evaluation of anthropogenic food consumption by urban wildlife and allow more detailed and in-depth studies of urban ecology.

2.3 Methods

Between February 2018 and January 2019 I obtained 33 hair samples from red fox carcasses from 16 geographic areas across the United Kingdom.

The collection was done opportunistically rather than systematically by

The collection was done opportunistically rather than systematically by correspondence with local contacts, primarily gamekeepers and town council refuse collection teams. From each location I collected paired samples from urban and rural foxes within a maximum radius of 20Km from each other (Figure 1.1, Table 1.1). The sex of the individual and the cause of death was also recorded. All hair samples were analysed for δ^{13}C, δ^{15}N and δ^{34}S at the Scottish Universities Environmental Research Centre (SUERC) stable isotope laboratory, East Kilbride, United Kingdom, in March 2019. Prior to the analysis, each sample was washed twice in a 2:1 chloroform: methanol solution, then rinsed with deionised water, in order to remove surface oils. The samples were then dried overnight at 60°C. The samples were then homogenised either by grinding them to a fine powder using a ball mill mixer, or cut into small sections with surgical scissors, depending on the amount of sample available. Finally, approximately 1.2mg of sample was weighted into tin capsules. The samples were combusted and analysed by continuous-flow isotope ratio mass spectrometry (an Elementar PYRO Cube linked to an Isoprime, now Elementar, Vision Mass Spectrometer).

International standards (IAEA-S1, IAEA-S2 and IAEA-S3 for sulphur, and USGS 40 for carbon and nitrogen) were included in the measurements to take into account the machine measurement fluctuations and standardise the results (Slater *et al*, 2001).

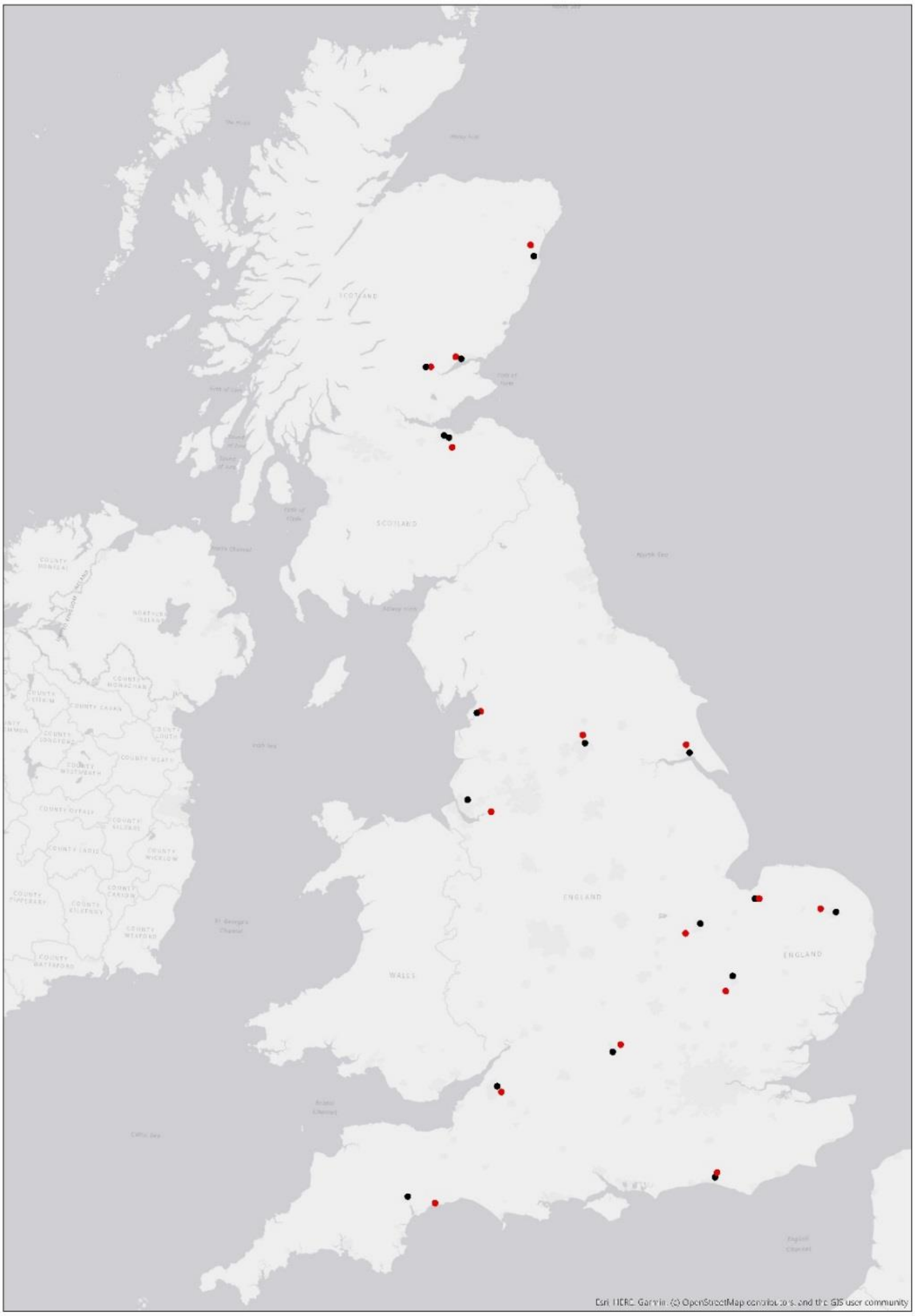

Figure 1.1 – Map of the United Kingdom showing the 16 sites of collection for the pair rural and urban red fox hair samples (33 samples in total). The rural sites are shown in red dots, while the urban sites are in black.

Date	Collection Area	Locality Name	Origin	Sex	Cause of Death
26/02/2018	Edinburgh	Gortonlee	R	F	Shot
06/03/2018	Perth	Dupplin	R	F	Shot
07/03/2018	Edinburgh	Gorgie	U	M	Roadkill
31/03/2018	Dundee	Balruddery	R	M	Shot
14/04/2018	Dundee	Ninewells	U	*NA*	Roadkill
21/04/2018	Exeter	Whipton	U	*NA*	Roadkill
30/04/2018	Bristol	Siston	R	M	Shot
07/05/2018	Bristol	Frenchay	U	F	Roadkill
12/05/2018	Cambridge	Barrington	R	F	Roadkill
16/05/2018	Lancaster	Knots Wood	R	F	Shot
19/05/2018	Brighton	Hollingbury	U	M	NA
23/05/2018	Leeds	Weardley	R	F	Shot
16/06/2018	Cambridge	King's hedges	U	M	Roadkill
25/06/2018	Exeter	Dunscombe	R	M	Roadkill
04/07/2018	Perth	Letham	U	F	Shot
14/07/2018	Lancaster	Moorlands	U	M	Shot
18/09/2018	Oxford	Iffley	U	*NA*	NA
23/09/2018	Leeds	Lidgett Park	U	*NA*	Roadkill
24/09/2018	Liverpool	Croxteth	U	M	Roadkill
04/10/2018	Liverpool	Moss Wood	R	M	Shot
13/10/2018	Peterborough	Elton	R	M	Roadkill
14/10/2018	King's Lynn	North Lynn	U	F	NA
20/10/2018	Norwich	Mousehold Heath	U	F	Shot
28/10/2018	Aberdeen	Hilton	U	*NA*	Roadkill
13/11/2018	Aberdeen	Lairshill	R	M	Shot
16/11/2018	Norwich	Poetsbreck	R	M	Shot
06/12/2018	Oxford	Stanton Wood	R	M	Shot
11/12/2018	Hull	East Park	U	*NA*	Roadkill
14/12/2018	King's Lynn	Mintlyn Wood	R	*NA*	Shot
26/12/2018	Peterborough	Dogsthorpe	U	F	NA
30/12/2018	Hull	Fairholme	R	M	Shot
10/01/2019	Brighton	High Park Farm	R	M	Shot
01/10/2018	Edinburgh	King's buildings	U	*NA*	Roadkill

Table 1.1 – Complete list of the 33 hair red fox hair samples that were analysed; including site, sex of the animal (if known) and cause of death.

Additionally, three laboratory internal standards were analysed every 10 samples to ensure the accuracy and precision of the analysis and to control for instrument drift: MSAG2 (methanesulfonamide), M2 (methionine mixed with ^{15}N enriched alanine) and

SAAG2 (sulphanilamide mixed with ^{13}C enriched alanine), all mixed with gelatine. Different sized aliquots of MSAG2 lab standard were used to correct for mass spectrometer linearity effects.

All stable isotope ratios are expressed in per mille (‰) using the δ notation:

$\delta X = [(R_{sample} / R_{standard}) - 1] \times 1000$

Where X is either ^{13}C, ^{15}N or ^{34}S and R is the corresponding ratio of heavy/light isotope: $^{13}C/^{12}C$, $^{15}N/^{14}N$ or $^{34}S/^{32}S$.

Out of the 33 red fox hair samples, I was only able to analyse 30, as one sample was lost during the processing phase while another two were lost in the furnace. However, the balance between urban and rural samples was maintained with 15 samples from each category.

In order to determine whether life in the urban environment has a measurable effect on the stable isotope ratio found in fox hairs, I used a series of linear mixed models (LMM). I fit a model for each isotope ratio using δX as a response variable and the urbanity level (rural/urban) as a binary predictor. In addition, I controlled for variation due to geographical distance, and so I fit geographic area as a random effect. The statistical analyses were all performed in R, and the model were fit using the lmer function from the package lme4. I also used the package SIBER (Jackson *et al.*, 2019) to visualise the stable isotope niche; this is described by Newsome *et al.* (2007) as “an area (in δ -space) with isotopic values (δ -values) as coordinates”; this is in practice a representation of the breath of the diet of an individual (or a group of individuals), according to the type of isotopes measured in the diet.

The isotope niche provides a bivariate measure (in the form of an ellipse) of the distribution of the individuals according to their origin group, each ellipse encompassing ~95% of the data (Jackson *et al.*, 2011).

2.4 Results

None of the isotope ratios, was significantly different between red fox hair samples from urban and rural locations (Table 1.2).

		Fixed effects	Estimate	SE	t-value	p-value
$\delta^{13}C$						
Random		*Intercept*	8.719	0.06514	133.861	
Effect (Var)	0.015	*Origin*	-0.025	0.08335	-0.311	0.758
$\delta^{15}N$						
Random		*Intercept*	-23.953	0.1498	-159.928	
Effect (Var)	0.208	*Origin*	0.103	0.1425	0.725	0.475
$\delta^{34}S$						
Random		*Intercept*	6.681	0.109	60.847	
Effect (Var)	0.068	*Origin*	0.026	0.129	0.208	0.837

Table 1.2 - Results of the LMMs fit to evaluate the effect of the origin of the sample (urban vs rural) on the stable isotope ratio of carbon, nitrogen and sulphur.

The graphical representation of the isotopic niche also confirmed that there was no noticeable difference between the two groups (Rural/Urban; Figure 1.2), for any combination of two elements.

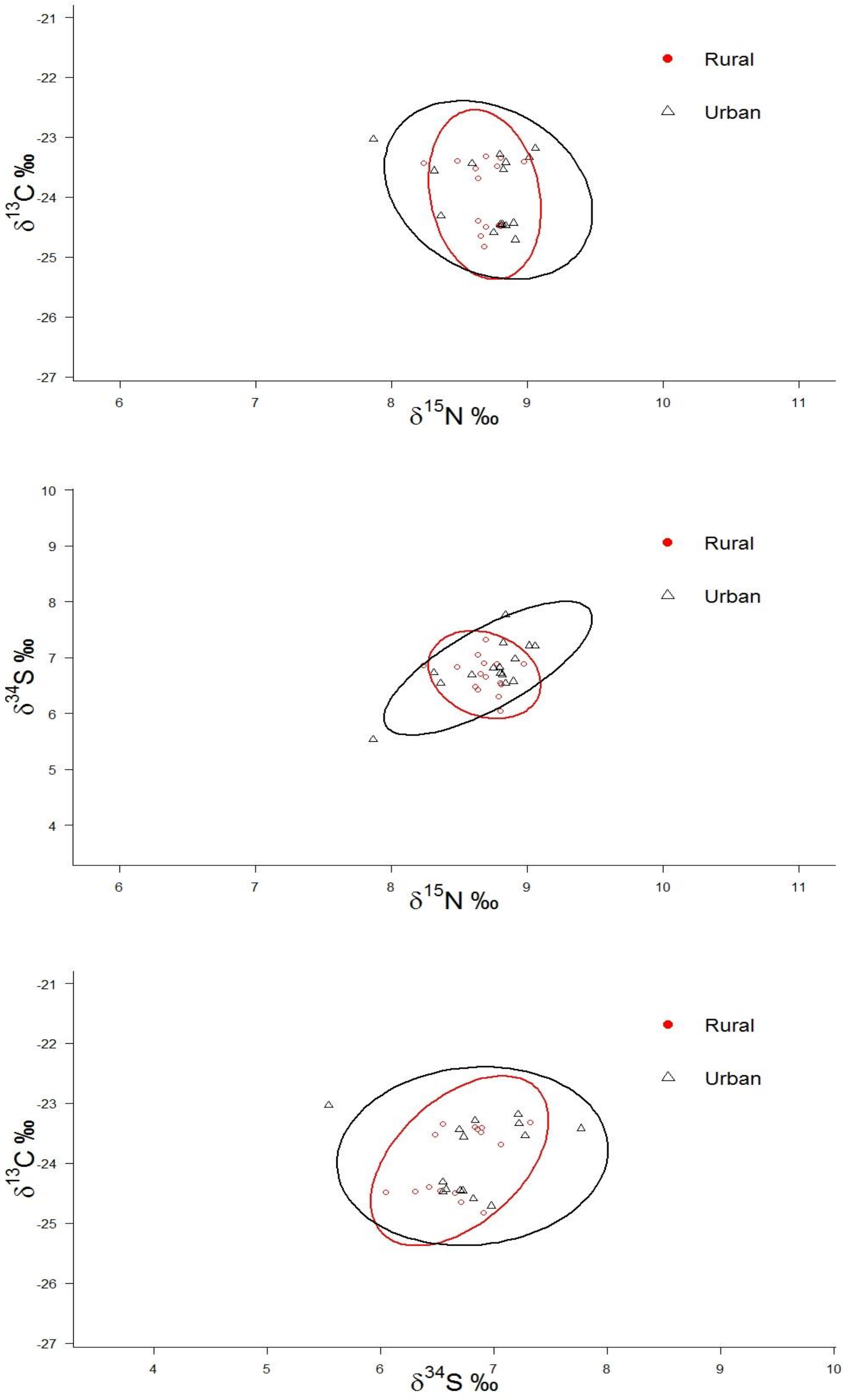

Figure 1.2 - Isotopic niches for the rural (in red) and urban (in black) fox origin groups. The three plots represent the combination of δ^{34}S and δ^{13}C values, showing the niche width for each combination; ellipses are calculated to include 95% of the data for each group.

2.5 Discussion

While it is becoming increasingly important to understand and accurately measure the impact of anthropogenic food as sources for wildlife, especially in urban habitats, this investigation found no detectable difference between the stable isotope ratio of urban and rural foxes; this suggests that SIA is not likely to be a suitable method to distinguish between the diet of urban and rural carnivores outside of locations where the human diet is significantly corn-based. The unique composition of North American processed food products allows for the detection of a higher $\delta^{13}C$ in individuals that have consumed a greater proportion of anthropogenic-sourced food (Jahren and Kraft, 2008). In this study I could not find any significant difference in $\delta^{15}N$, which has been shown to be an effective indicator of a more anthropogenic diet in urban blue tits (Pollock *et al.*, 2017). These results indicate that SIA either may not be a suitable candidate for evaluating the grade of anthropogenic food consumption in the diet of European (or at least British) foxes, or that the pair geographical samples of red foxes form rural and urban sites did not differ in their anthropogenic diet consumption.

The analysis is based on the assumption that urban foxes would have more access to anthropogenic food sources (Harris, 1981c; Contesse *et al.*, 2004), but I do not have a direct measurement of the anthropogenic food consumption for individual foxes. Given the heavily human dominated landscape of rural Britain (Eigenbrod *et al.*, 2009), it is possible that the diet of foxes that I considered rural, is in reality not very different from that of foxes living in urban locations. In other words, even if SIA is capable of measuring differences in amount of anthropogenic food consumed by foxes, there might not be a significant difference between the pair sites. Given these results, I was not able to include anthropogenic food consumption as a variable in further analysis presented in this thesis, including parasite infection and intensity.

Given these limitations, further studies should take a more rigorous approach in selecting the samples to analyse: using hair samples from foxes with a known diet (e.g. captive animals), or individuals with a known territory (such as GPS collared animals) would help distinguish more rigorously between urban foxes, consuming significant amount of anthropogenic food, and rural ones, with a more natural diet.

2.6 Acknowledgements

The samples used in this analysis were sourced from all over the UK, I would like to thank my supervisor, Matt Bell, for coordinating the collection of the samples; this analysis would not have been possible without your help.

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Chapter 3

Fine-scale variation in the urban landscape affects marking patterns and gastrointestinal parasite diversity in red foxes.

Co’ la volpe convien volpeggiare.

Tuscan proverb

3.1 Abstract

Urban areas are considered to be a hostile environment for wildlife as they are often highly fragmented and frequently disturbed. However, these same habitats can also contain abundant resources, while lacking many common competitors and predators. Urban environments can both directly impact the species living there, but can also have indirect effects mediated by their parasites and pathogens. Yet, few studies have taken into account the spatial heterogeneity of urban landscapes, which can be important for parasite transmission and persistence.

Here I investigate how fine-scale variation in the urban environment can affect gastrointestinal (GI) parasite infection risk and community structure in red fox (Vulpes vulpes) populations across the city of Edinburgh (UK). I surveyed all green spaces across the city to determine the influence of both socio-economic and ecological variables on fox marking behaviour, GI parasite prevalence and parasite community diversity. I found that the presence and abundance of fox faecal samples were non-uniformly distributed, and instead was dependent on the ecological characteristics of a site. Specifically, foraging areas were left largely unmarked, indicating that availability of suitable resting and denning sites may be a limiting factor in urban environment. In addition, the amount of green space was positively correlated with overall GI parasite prevalence, species richness and diversity, highlighting the importance of greenspace (a measurement of landscape connectivity) in urban areas in determining the composition of the parasite community.

These results suggest that fine scale variation in the urban environment can be important for understanding the ecology of infectious diseases in urban wildlife and could have wider implication for the management of urban carnivores.

3.2 Introduction

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

Ecological species assemblages, or communities, that exist in urban environments tend to have a different composition from those found in wild settings (Aronson *et al.*, 2016), but they are not necessarily less diverse (Parsons *et al.*, 2018). Urban communities often consist of species capable of tolerating highly disturbed habitats, and able to exploit novel resources (Luniak, 2004). While there is an increasing focus on understanding the ecological communities that emerge in urban areas, the consequences for how the urban landscape may impact the parasite community, defined broadly here to include both macro-parasites (e.g. helminths, arthropods, etc.) and microparasites (e.g. viruses, bacteria, protozoans, etc.), that infect these species remains unclear (Bradley and Altizer, 2006). For this reason understanding the factors driving parasite diversity, infection risk and parasite burdens in urban wildlife can be important to unravel the dynamics of transmission at the wildlife-human and urban-wild interfaces (Gortázar *et al.*, 2007). For example, previous research in rodent communities has shown that the fragmented landscape and associated decrease in biodiversity found in urban areas is correlated with an increase in the density of white-footed mice (*Peromyscus leucopus*), which are very competent hosts for the spirochete bacteria (*Borrelia burgdorferi*) that cause Lyme disease. This has been suggested to increase infection risk for humans in these urban areas (Rizzoli *et al.*, 2014). 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 parasite 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 how urbanisation will impact 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 and Altizer, 2006). A clear example of this variation has been demonstrated in 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 human populations 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). Long-term monitoring programs are in place across central Europe to record changes in the prevalence and distribution of *E. multilocularis*, including extensive culling programs in some cities

(Contesse *et al.*, 2004). In a review of *E. multilocularis* in urban fox populations, Deplazes *et al* (2004) concluded that urban foxes have a lower proportion of small rodents (the intermediate hosts) in their diet, leading to lower infection prevalence 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 small settlements in rural China, a pattern that was hypothesised to be driven by the presence of free-roaming dogs, a key definitive host for *E. multilocularis,* (Liccioli *et al.*, 2015).

These contrasting results 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 incorporate this intrinsic variability, is difficult (Weeks, 2010). In fact, most studies to date, used subjective classifications to identify specific environments within urban areas, generally attempting to define an urban vs rural contrast (see for example Prange *et al.*, 2003; Fischer *et al.*, 2005; Reperant *et al.*, 2007a; Robardet *et al.*, 2008). However, “urban” and “rural” are just ends of a continuous spectrum, and to understand the dynamics and structure of parasites communities in urban environments, it is important to be able to classify specific characteristics of urban areas or ‘urbanity’ along this spectrum. These metrics need to be objective, quantitative and capture the heterogeneity and fragmentation of the urban environment on a fine scale, while also being able to accurately characterise the rural-urban transition within continuous, multivariate space.

Predators, especially large carnivores, are generally unable to establish resident populations in urban areas, as they tend to be large-bodied, highly mobile, and require large territories (Fuller *et al.*, 2010). Because of these ecological characteristics, predators are also often in conflict with humans (Curtis and Hadidian, 2010b) and actively persecuted in inhabited, urban areas. However, mesocarnivores (medium sized carnivores that tend to have a more flexible diet)such as foxes and raccoons, can thrive in urban areas because of abundant anthropogenic food resources, often reaching high population densities that would be unsustainable in wild habitats (Bateman and Fleming, 2012). Red foxes in particular are extremely adaptable, (Harris and Baker, 2001), with a generalist diet (Contesse *et al.*, 2004), high reproductive potential (Pagh *et al.*, 2018) and a flexible social system (Iossa *et al.*, 2008); these traits allow foxes to adapt to urban environments and quickly establish dense population sizes (Harris, 1981a; Janko *et al.*, 2012). Records from the early 1900s in London, United Kingdom suggest that urban fox populations were already well established (Teagle, 1967). Patterns of long-standing urban fox populations have been reported in numerous countries, particularly in Canada, Australia, Japan and in mainland Europe (Harris and Rayner, 1986; Adkins and Stott, 1998; Gloor *et al.*, 2001; Marks and Bloomfield, 2006; Uraguchi *et al.*, 2014). However, urban foxes have often been regarded as pests because they can carry important zoonotic diseases (e.g. rabies virus, *E. multilocularis*) which generate concern for public health (Reperant *et al.*, 2007b; Comte *et al.*, 2013; Laurimaa *et al.*, 2016).

Here, I developed a multivariate, continuous measure of ‘urbanity’ in order to investigate the effect of fine scale habitat changes on the abundance of foxes and the composition of their gastrointestinal parasite communities across the urban areas of Edinburgh, UK. To do this, I conducted an extensive non-invasive survey of public greenspaces across the entire urban area of Edinburgh, recorded all red fox scats to identify fox distribution patterns, and then analysed the samples in order to identify and quantify the gastrointestinal parasite community composition. I used fine spatial scale metrics that included both human socio-economic variables (i.e. human population density, traffic counts, greenspace, etc.) and ecological variables (i.e. presence of other wildlife species, habitat characteristics, etc.), to capture the complex biotic and abiotic structure of the urban environment and investigate their relationship with parasite diversity and infection prevalence. My goal is to identify variables that are important drivers for urban wildlife infectious disease, in order to provide an objective and easily quantifiable measure of urbanity in order to improve comparability and repeatability of urban disease ecology studies.

3.3 Methods

3.3.1 Study area and survey design

Fieldwork was carried out in the urban area of Edinburgh, United Kingdom (55.9533° N, 3.1883° W); I identified study sites using the greenspace database (http://digimap.edina.ac.uk/os). Specifically, I selected all areas classified as public greenspaces (i.e. public parks, playgrounds, golf courses, open semi-natural areas, etc.) within the city limits. In total, this included 329 unique sites, varying in size between 0.0002 km^2 and 1.684 km^2; with an average site area of 0.135 ± 0.22 km^2. Of this set of greenspaces, I was 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 213.35Km^2, and the surveyed sites covered 16.7% of the total area (Figure 3.1).

I surveyed each greenspace site twice in 2017. The two sampling periods were chosen to capture differences in fox life history: i) the “Spring” season (25th January to 4th May 2017) coincided with the period between breeding and the 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, I 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, I 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.

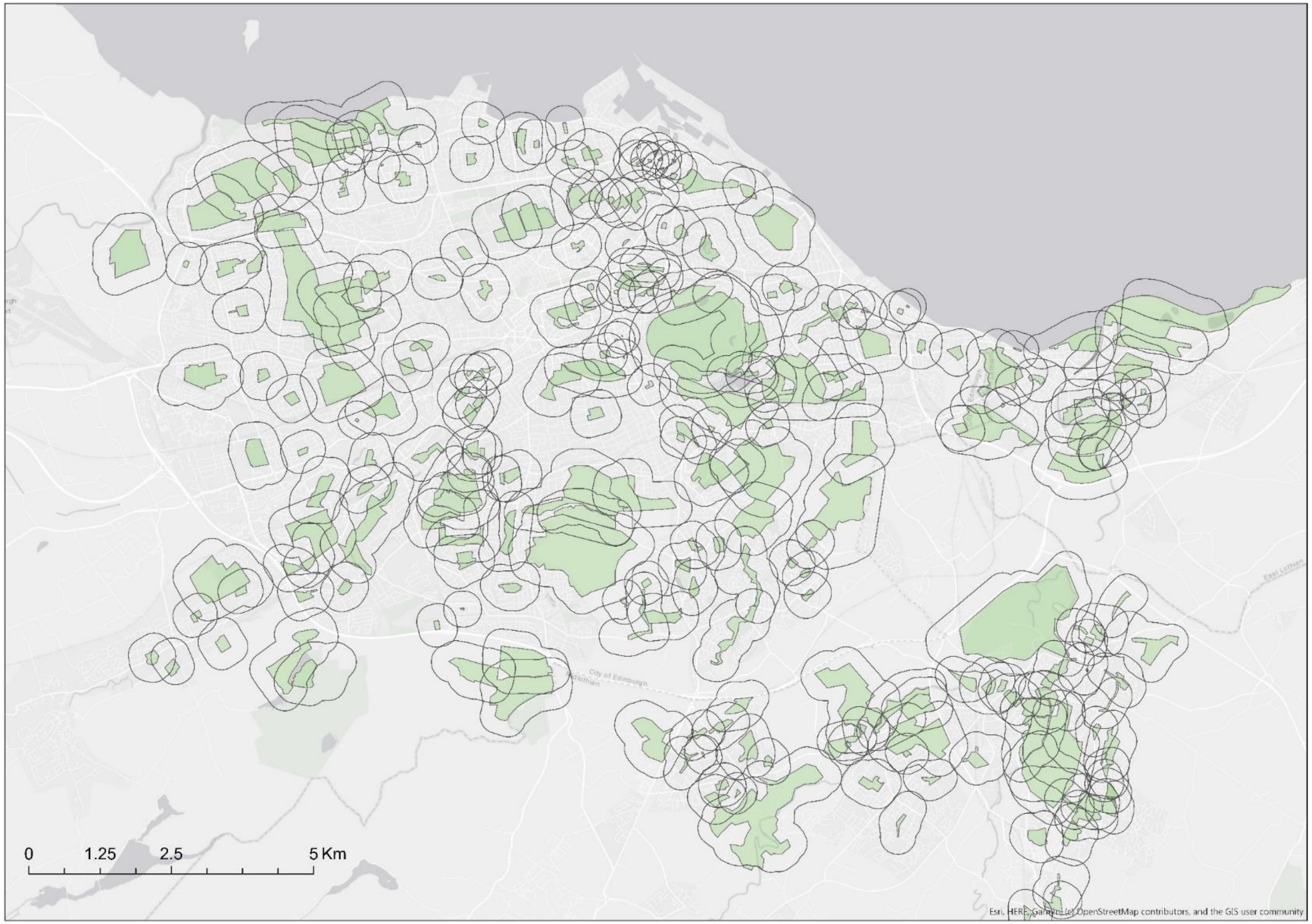

Figure 3.1 – Map showing the 273 survey sites (in green), which were sampled during the two survey periods (Jan to Apr - Aug to Oct) in 2017. The map also includes the buffers constructed on a 300 m planar radius around each one.

3.3.2 Socio-economic and ecological variables

In order to effectively capture fine scale variation in the urban landscape, I measured both socio-economic and ecological variables. First I identified several ‘socio-economic‘ variables that reflect aspects of anthropogenic disturbance that are typically representative of “urbanity” (Hahs and McDonnell, 2006): human population density, roads and traffic counts, and the ratio and variability of space (Figure 3.2). I 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 and 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 and Bauer, 2007; Gaston *et al.*, 2010) and their distribution correlates with habitat disturbance (Arnold and Gibbons, 1996). Traffic is the leading cause of fox mortality in cities (Gosselink *et al.*, 2007) which can generate marked changes in the demographic structure of urban fox populations (Baker *et al.*, 2007).

(iii) Greenspace ratio and variability (http://digimap.edina.ac.uk/os). The most important urban areas for providing suitable sites for wildlife to rest and breed are likely found in ‘greenspace’. 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 and Hochuli, 2017). Greenspaces are vital to the survival of urban foxes (Baker *et al.*, 2007), which are primarily active during the night and require safe hiding spots to rest during the day (Harris and 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 and Horn, 1997). Greenspaces can indicate very different kinds of landscapes, i.e. publicly vs privately owned land, or parks vs playgrounds and these different habitat types will not all prove suitable for foxes to live in; thus, I included greenspace variability (number of different kind of greenspace) in this analysis along with the greenspace ratio (greenspace/total area).

For each greenspace site surveyed, I also recorded the following four ecological variables that describe important aspects of the biotic habitat:

(i) Presence/absence of European rabbits (*Oryctolagus cuniculus*). These medium-sized (2-4kg) lagomorphs are one of the main prey species of red foxes (Lees and Bell, 2008) and are present across Edinburgh.

(ii) Presence/absence of roe deer (*Capreolus capreolus*). The presence of large ungulates, such as roe deer, while not directly related to fox diet as they are too large to be prey, serve as a useful proxy indicator for the overall ‘wildness’ or scale of the urban habitat suitable for wildlife of a site (Magle *et al.*, 2014).

(iii) Presence/absence of European gorse (*Ulex europaeus*). The vegetation of this plant, which is found across both urban and rural habitats across the UK, is particularly impenetrable. This dense vegetation can create secure, suitable microhabitats within human-dominated or disturbed green spaces where foxes, and other urban wildlife, may safely rest and breed (White *et al.*, 2006).

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(v) Vegetation management regime. This can vary from high intensity amenity grassland to very low intensity semi-natural woodland or moorland, with likely consequences for prey abundance and diversity (Goddard *et al.*, 2010), the availability of resting and denning sites, and the extent of human incursion and disturbance. I assessed this index as the intensity of the management rather than its extent, on a scale from 0 (the site vegetation was left completely untouched), to 4 (large portions of the site were actively managed throughout the year; e.g. by cutting the grass).

Each socio-economic variable defined above was mapped across the entire study area using a 25mx25m raster ArcGIS pro 1.4 (ESRI, 2017); I extracted the average value relative to each site using the zonal statistics tool. For the greenspace variability metric, I obtained both the average greenspace cover (i.e. ratio of green area/total area) and the variability of green space, which is expressed as the number of different green space categories (out of the 25 identified by remote sensing in the dataset).

Given the estimates of urban fox home ranges (~1.75Km^2 for resident adults; Castañeda *et al.*, 2019), it is likely that foxes living in a specific greenspaces 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, I 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 at different scales, thus I standardised each to a mean of zero and variance 1 to avoid convergence problems in the models.

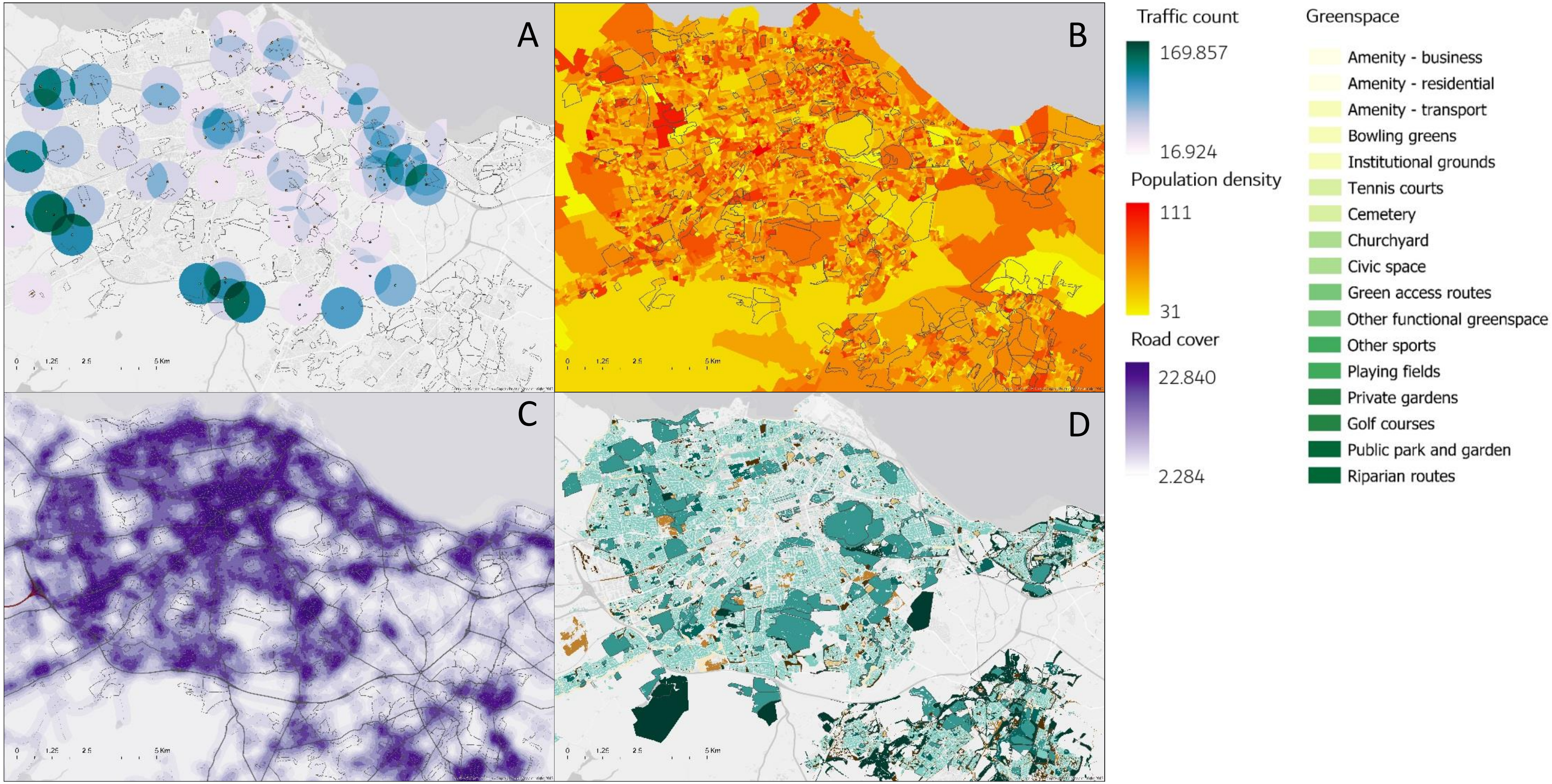

Figure 3.2 – Maps that show the range and distribution of the four socio-economic datasets used in the analyses. A) Traffic counts, expressed in average number of vehicles per day. B) Population density, expressed in number of people per hectare. C) Road cover, expressed in Km of road per Km. D) Greenspace, mapped according to the classification of the original dataset (OS open greenspace). All four datasets are mapped using a 30mx30m raster and the data relative to each site (plotted in grey in each map) surveyed are extracted as average of pixel value within a 300m planar buffer area around each site (see figure 3.1).

3.3.3 Gastrointestinal parasite community

All fresh fox faecal samples were analysed using salt flotation and microscopy in order to identify each parasite species based on the morphology of eggs and oocysts. To ensure accurate measures of parasite infection and burden (number of eggs/oocysts per gram), every faecal sample was divided into 4 sub samples, and each sub-sample was weighed and then assessed via salt floatation. Parasite presence/absence (0/1) or 'infection risk' was defined as 1 or more positive subsamples; while parasite burden (number of eggs/oocysts per gram of faeces) was calculated by dividing the total number of eggs/oocysts found across the four readings by the weight of the sample in grams. Parasite species were identified using the Veterinary Parasitology Atlas (Foreyt, 2001) and previously reported gastrointestinal parasite infections of red foxes in the UK and Ireland (Thompson, 1976; Hackett and Walters, 1980; Richards *et al.*, 1995; Wolfe *et al.*, 2001; Smith *et al.*, 2003; Murphy *et al.*, 2007; Morgan *et al.*, 2008; Stuart *et al.*, 2013; Learmount *et al.*, 2015). When possible, I identified each parasite to the species level, however it some cases this was not possible and so I identified each parasite to the lowest taxonomic level possible. For each faecal sample I recorded (i) presence/absence (0/1) for each parasite species, (ii) species richness (number of GI parasite species) and the (iii) Shannon diversity index, calculated for each faecal sample using the parasite infection risk and burdens. Specifically, the Shannon diversity index (H) was calculated using the package vegan (Oksanen *et al.*, 2015), according to the formula:

$$H = -\sum_{i=1}^{I} p_i \ln p_i$$

Where p_i is the proportion of individuals belonging to the i^{th} species. 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).

3.3.4 Statistical analysis

To investigate the influence that urbanity had on the distribution of fox scats and the gastrointestinal parasite community composition across the urban environment of Edinburgh, I fit a series of generalised linear mixed models (GLMMs). These models tested how the socio-economic and ecological variables defined above impacted (i) scat distribution (number of scats found per site), (ii) parasite species richness, (iii) parasite community composition (Shannon diversity index). Finally, I also fit individual models to test the effect of socio-economic and ecological variables on single parasite species infection risk (presence/absence). I did not run model including parasite burden (egg per gram) as the values fluctuated significantly between subsamples, and I cannot confidently say that these values were representative of the real parasite burden of each individual fox.

I first tested for evidence of spatial autocorrelation in using a variogram of the Pearson's residuals from each model. All models showed evidence of spatial autocorrelation so all models were fit to also include a spatial term using a conditional autoregressive correlation model with a Matérn correlation structure (Rousset and Ferdy, 2014). The package spaMM (Rousset *et al.*, 2018) was used to fit the GLMMs with the spatial effect. 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, I also checked for collinearity between the variables by calculating the variance inflation factor (Zuur, Gende, *et al.*, 2009), which provides an index that measures how much the variance of the estimated regression coefficient is increased because of collinearity. I used a value of 2 as cutoff for exclusion (following Craney and 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 I 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 species that were recorded at each site.

Each model included the following fixed effects measured at the site plus the 300m buffer: the five socio-economic variables (population density, road cover, traffic counts, greenspace ratio and variability – all continuous with a mean of 0 and variance of 1) and the two ecological variables, urban wilderness and the level of vegetation management. I also included the sampling period as a factor (Spring and Autumn), site area (m^2; log transformed), and site transect length as an offset (to account for the different transect lengths in each site; continuous; m) in each model. The model to test the factors affecting the number of scats per site was fit using a Poisson distribution and included Site ID and a Matérn spatial correlation structure as random effects. Next, to investigate the drivers of parasite species richness (count data) and the Shannon diversity index (H; continuous) I 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 species per sample), I fit 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.

3.4 Results

3.4.1 Red fox scat distribution across urban Edinburgh

Across the two sampling periods in 2017, I found 287 fox scats 144 in Spring and 143 in Autumn (Table 3.1). Overall 224 (78%) were collected for gastrointestinal parasite analysis: 118 and 106, respectively.

Fixed effects	Estimate	SE	t-value	p-value
Intercept	-12.029	1.885	-6.381	
Road Cover	0.040	0.222	0.182	
Traffic counts	-0.017	0.149	-0.118	
Population Density	-0.028	0.162	-0.174	
Green Space Ratio	**2.374**	**0.971**	**2.443**	*
Green Space Variability	0.021	0.025	0.821	
Sampling period (Autumn)	-0.373	0.212	-1.755	
Site Area (Log)	0.052	0.159	0.329	
Urban Wilderness (1)	**2.050**	**0.506**	**4.044**	***
Urban Wilderness (2-3)	**3.166**	**0.510**	**6.200**	***
Veg Management level (1-2)	-0.090	0.478	-0.189	
Veg Management level (3-4)	-0.570	0.433	-1.316	
Random effects	Variance			
Site ID	0.392			
Spatial effect	0.355			

*Table 3.1 - The GLMM output for what factors determine 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. * $p < 0.005$, ** $p < 0.001$, *** $p < 0.0001$.*

Red fox scats were found only in 50 of the greenspace sites (18.3%), and this pattern was consistent 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 4.042 ± 2.399 (Range = 1- 27; Jan – Apr = 4.114 ± 3.823; Aug - Oct = 3.972 ± 5.241), indicating that if a site was marked, it was likely to contain multiple scats. I found the number of fox scats found at a site was determined by both socio-economic and ecological factors. Specifically both the greenspace ratio (t = 2.4432, p = 0.0233) and the composite score called 'urban wildness' score, which is a count of the number of other important native species present (including the presence absence roe deer, rabbits and gorse; t = 4.0447 and t = 6.2009 respectively for the two levels, p < 0.0001; Table 3.2) both were significantly and positively associated with a the number of scats found.

3.4.2 Gastrointestinal parasites community

I identified six parasite taxa from the fox faecal samples collected across urban Edinburgh (Figure 3.3). Specifically, I found four helminth taxa, including three nematodes and one cestode, and two species of coccidian protozoan. Due to limitations with the analysis of just eggs/oocysts from faecal samples, the taxonomic resolution for parasite identification was variable. I was able to identify three parasitic helminths to species level: *Toxocara canis*, *Eucoleus aerophilus* and *Uncinaria stenocephala*, however, the other three taxa were identified to genera (helminth: Taenia spp. and coccidian protozoans: *Eimeria* spp. and *Isospora* spp.).

Figure 3.3 - The following gastrointestinal parasite taxa were identified as eggs or oocysts from Red fox scat samples collected across urban Edinburgh in 2017using faecal floatation and microscopy. a) Eimeria spp; b) Isospora spp; c) Euculeus aerophilus; d) Toxocara canis; e) Uncinaria stenocephala; f) Taenia spp. The magnification is the same for all pictures (40x).

Overall, 83.9% (118 out of 224) of the faecal samples contained helminth eggs or coccidian protozoan 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 overall prevalence of each parasite taxon found: infection with helminth parasites were more common (79% of samples had at least one taxon) than coccidian protozoans. (45.9%; Table 3.2). 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 3.2).

	Spring		Autumn	
Taxon	Prevalence	Burden	Prevalence	Burden
Eimeria spp.	42.8	24.59	30.8	199.57
Isospora spp.	10.1	0.24	17.7	2.08
Total Coccidia	47.0	24.82	43.0	201.65
E. aerophilus	52.1	1.08	32.7	3.13
T. canis	14.3	2.68	13.1	14.41
U. stenocephala	47.1	4.59	42.0	4.70
Taenia spp.	12.6	1.10	4.67	0.12
Total Helminth	82.3	11.32	72.9	11.82

Table 3.2 - 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 green spaces in urban Edinburgh in 2017, for each of the two survey seasons: Spring (January to April), and Autumn (August to October).

While there were several significant factors, greenspace was the strongest, most consistent predictor across all three GLMMS of GI parasite metrics. GI parasite diversity, as measured by the Shannon index, was positively associated with both greenspace ratio (t = 3.236, p = 0.00148) and variability in types of greenspaces (t = -2.264, p = 0.0246) while negatively associated with the second survey season, where autumn had a 38.4% reduction in GI parasite diversity (t = -2.297, p = 0.0259; Table 3.4).

	Shannon Index (H)				Parasite species richness			
Fixed effects	Estimate	SE	t-value	p-value	Estimate	SE	t-value	p-value
Intercept	0.04358	0.573224	0.07603		*1.016129*	1.37664	0.738122	
Road Cover	0.042897	0.033803	1.26903		*0.066237*	0.08021	0.825813	
Traffic counts	0.054477	0.027243	1.99964		*0.096439*	0.05655	1.70542	
Population Density	0.008353	0.027584	0.30282		*0.005118*	0.06321	0.08097	
Green Space Ratio	**0.77541**	**0.23913**	**3.24258**	**	***1.512695***	**0.56703**	**2.66773**	**
Green Space Variability	**0.02164**	**0.00955**	**2.26494**	*	*0.03479*	0.02255	1.542447	
Sampling period (Autumn)	**-0.1162**	**0.0506**	**-2.2974**	*	***-0.267182***	**0.11622**	**-2.299**	*
Site Area (Log)	-0.02506	0.13473	-0.18599		*0.00213*	0.31904	0.006676	
Urban Wilderness (1)	0.00521	0.112052	0.04649		*0.102583*	0.25943	0.395415	
Urban Wilderness (2-3)	-0.03023	0.069223	-0.4367		*-0.188897*	0.16435	-1.14939	
Managed Vegetation level (1-2)	-0.10694	0.108965	-0.9814		*-0.175261*	0.24995	-0.7012	
Managed Vegetation level (3-4)	-0.15711	0.093078	-1.68799		*-0.364019*	0.20276	-1.7953	
Random effects	Variance				Variance			
Site ID	6.52E-09				*7.21E-09*			
Spatial effect	0.00472				*8.33E-09*			

*Table 3.3 - Output for the two parasite diversity models, Shannon Index (left) and species richness (right). 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. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.*

Specifically, samples found in sites with a higher GS ratio and variability tend to have a higher GI parasite diversity.

Both the greenspace ratio (t= 2.668, p = 0.00764) and season (t = -2.299, p = 0.02150) were significant predictors of GI parasite species richness for the urban red foxes of Edinburgh (Table 3.3); both of these patterns were in the same direction as for GI parasite diversity.

Fixed effects	Estimate	SE	t-value	p-value
Euculeus aerophilus	1.246	2.296	0.542	
Taenia spp	-1.035	2.305	-0.449	
Toxocara canis	-0.508	2.300	-0.221	
Uncinaria stenocephala	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	
Green Space Ratio	**2.671**	**0.996**	**2.679**	*****
Green Space 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 3.4 - Model output of the Bernoulli model for the likelihood of infection (presence-absence) of parasites measured in each sample. I measured the infection status of each sample and controlled for parasite taxon in order to determine which variables in the urban environment are important in determining the likelihood of a fox to be infected by a GI parasite. 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*

Similarly, I also found that the greenspace ratio (t = 2.667729, p= 0.0076) and survey season (t = -2.299020, p=0.0215) were significant predictors of the likelihood of GI parasite infection, measured as the presence/absence of each parasite taxon in the same model, with parasite taxon fitted as a fixed effect (Table 3.4). Consistently with the models on gastrointestinal parasite diversity and species/taxon richness, I found that survey areas with more greenspace had significantly higher likelihoods of infection across all parasite taxa, while the later autumn sampling period had lower infection rates.

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, I ran models evaluating the overall coccidian prevalence (inclusive of both coccidian taxon). The models do not show any overall trend (see appendix 3, Table A3.1 for the full output of the models), Greenspace is positively correlated with the prevalence of *U. stenocephala* (t = 2.0371), but with no other parasite taxon taken into consideration; *E. aerophilus* was less prevalent in the second survey season (t= -3.199) and both *E. aerophilus* and the coccidian parasites prevalence was correlated with the level of urban wilderness, but in opposite direction (t = -1.616 and t = 1.835 respectively). None of the variables included in the model had a significant effect on the prevalence of *T. canis*.

3.5 Discussion

These results suggest that fine-scale variation in urban landscapes plays an important factor in determining both fox marking patterns and parasite community composition. In particular, Greenspace ratio was positively associated with the number of fox scats found in a site, parasite diversity, species richness and likelihood of infection; well-connected sites were more heavily marked and had higher prevalence of parasites, as well as a larger and more diverse parasite community.

I found a distinct, highly localised, distribution of scats where more natural sites tended to be heavily marked (Figure 3.4), while more urban sites were left completely unmarked, with the 'wilderness' metric being the single strongest predictor of the number of

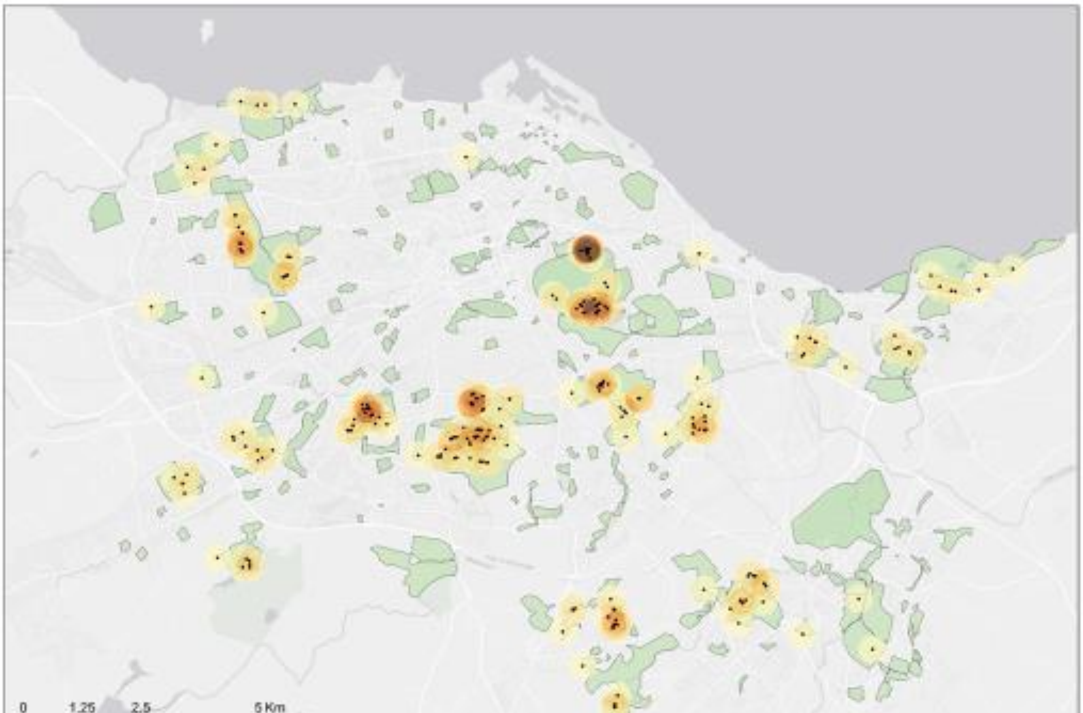

Figure 3.4 - Map of the study area (urban Edinburgh), highlighting all the survey sites in green (n=273; 16.7% of the entire map area). All Red fox scats that were found across both seasons are represented by black dots. The density of scats across the area is mapped using a kernel density function with a radius of 300m. The colour represents the number of scats found per square metre from dark orange to transparent (min =0.00024, max=0.0255).

fox scats found (Figure 3.5). This is unexpected because foxes have been previously shown to mark uniformly throughout their territory (Macdonald, 1980). One interpretation is that these are the only areas frequented by foxes, with the rest of the city left vacant. However, most of the marked sites are considerably smaller than the reported size of fox home ranges (Castañeda *et al.*, 2019), even considering that urban foxes' home ranges are smaller than rural ones (0.115 - 0.458 Km^2 ; Marks and Bloomfield, 2006). Therefore, foraging territories are likely to extend beyond the boundaries of the park, yet do not appear to be marked. Moreover, Kolb (1985) reported extensive use of some habitat types in Edinburgh that I found completely unmarked (e.g. cemeteries). This was confirmed by my own observation (Gecchele *et al,* unpub data) of foxes roaming and foraging on unmarked sites at night.

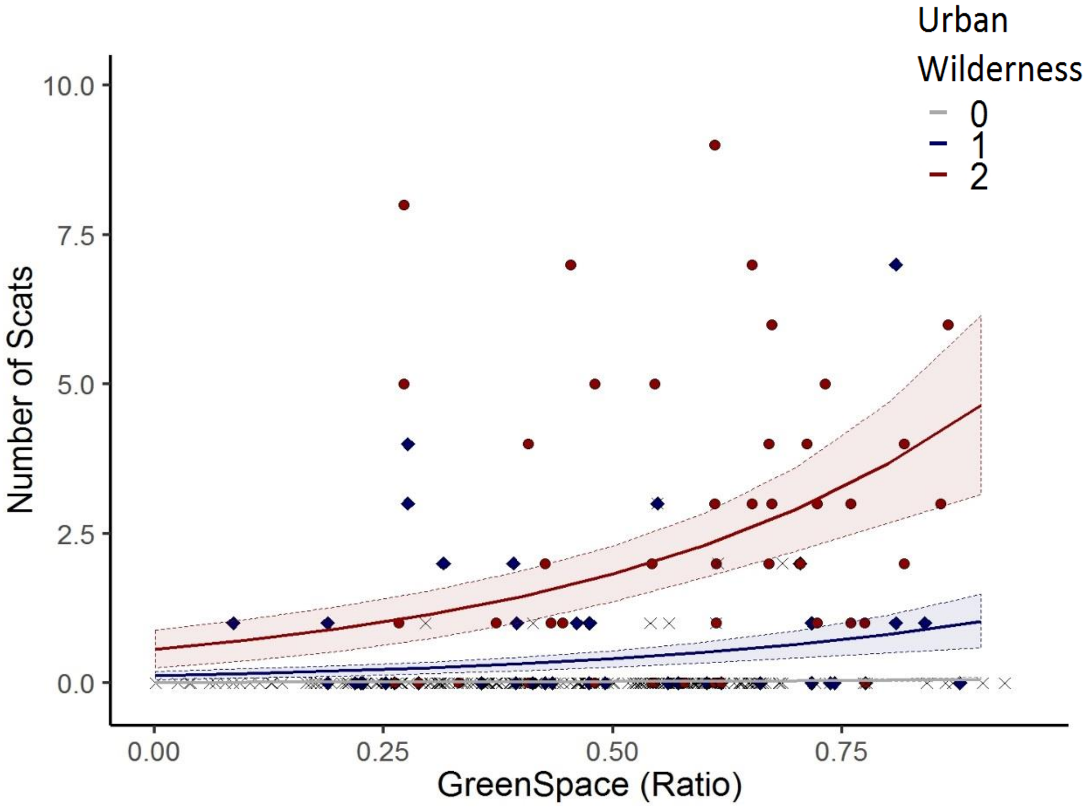

Figure 3.5 - Model prediction from the GLMM on number of Red fox scats found per site. Greenspace ratio was positively associated with the number of scats found, I also found a positive relationship with 'urban wildness' score, with a higher number of fox scats found in sites where I record the presence 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.

In light of these results, an explanation for the observed scat distribution pattern is that marking is most concentrated in sites that are suitable for resting and denning, and that there may be intense competition for control of these sites, which may drive the intensive marking regime I observed. Previous work has shown that (peri-)urban foxes display a preference for resting sites either in rural settings (woodland or reed beds), or sites offering sufficient protection from disturbance (e.g. dense vegetation; (White *et al.*, 2006; Janko *et al.*, 2012). Furthermore, other studies on urban foxes from Bristol showed that resting site fidelity is much higher when fox population densities are high (and decreased sharply following a mange outbreak that decimated the fox population in the city; Newman *et al.*, 2003). High densities of scats in specific sites may have important consequences for the parasite ecology of the foxes, significantly increasing the infective pressure on the foxes occupying the site. Previous studies have shown how the clumping of individuals (and hence increased frequency of latrines) increase the prevalence and species richness of gastro intestinal parasites in raccoons (Wright and Gompper, 2005) compared to individuals living at similar densities, but with a less pronounced clamped marking behaviour.

These results show that greenspace ratio is the single most important predictor for both parasite diversity, species richness and prevalence, being positively correlated with all these three metrics (Figure 3.6). Greenspace ratio is effectively a measurement of landscape connectivity since foxes can use greenspaces to move safely across the urban environment (Kolb, 1984). Lower levels of Greenspace ratio could limit fox movement (both during juvenile and adult territorial movement); this, in combination with access to high levels of food sources, allows relatively small territories to sustain large family groups (Baker *et al.*, 1998, 2004). This isolation could result in lower exposure to parasites, hence decreasing parasite prevalence and diversity.

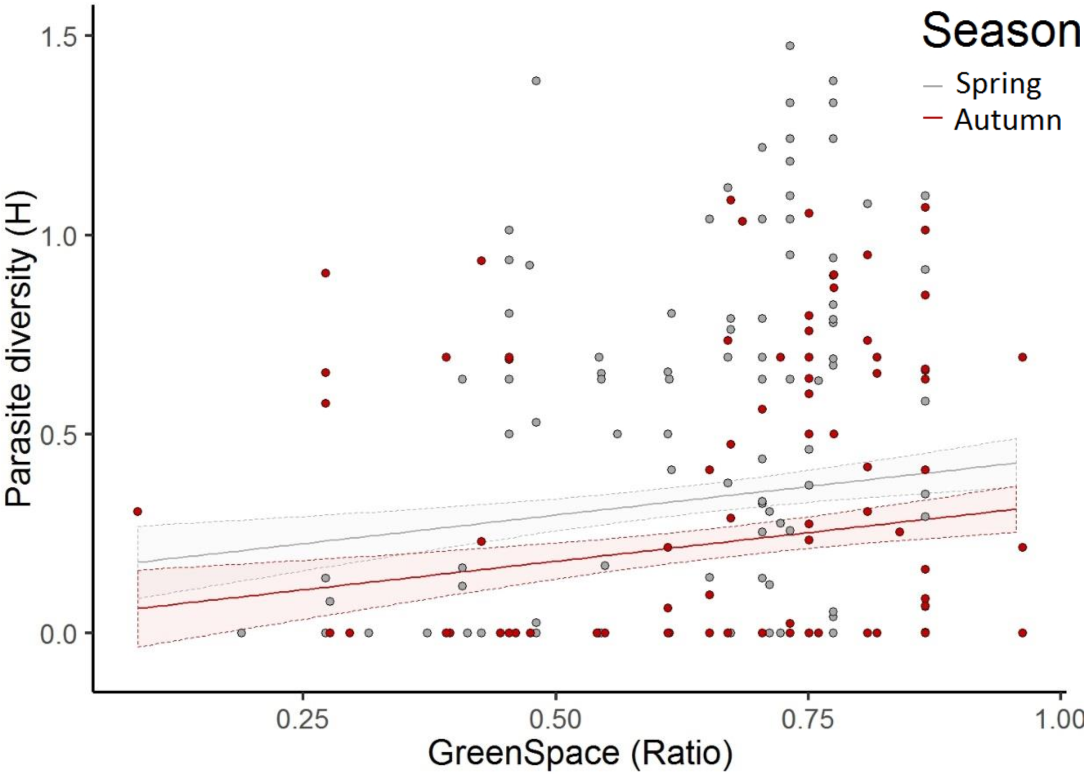

Figure 3.6 - Model predictions from the GLMM on parasite Shannon diversity measured per fox faecal sample. The greenspace ratio was positively associated with the Shannon diversity index (on the x-axis); Season also had an effect, with samples from the second season (in red, August to October) having a lower parasite diversity compared to the first (in grey, January to April). Lines show the model predictions; the raw data is also included in the figure as specific points, in the same colour scheme.

A recent study conducted on foxes from Berlin (Gras *et al.*, 2018) produced results compatible with my own: the study focused on the effect of urban landscape structure on the seroprevalence of canine distemper virus (CDV) on fox carcasses collected around the city. Their results indicated that the amount of greenspace in the area surrounding the carcass was positively correlated with the probability of seropositivity, but only for juvenile animals; they concluded that access to more greenspace for juveniles was associated to a higher potential for dispersal and hence a higher risk of disease transmission.

To the best of my knowledge, this is the first study to find a link between landscape fragmentation and prevalence of soil-borne parasites: most studies tend to focus on the effect of resource abundance and distribution (see for example Bradley and Altizer, 2006;

Mackenstedt *et al.*, 2014) on the disease ecology of urban mammals, disregarding the potential role of landscape fragmentation. However, I argue that including a measure of landscape fragmentation in urban disease ecology studies could be a more effective way to capture meaningful effects on ecological communities than resource availability. For example, human density population has been shown to be positively correlated with the amount of anthropogenic food available to urban foxes (Contesse *et al.*, 2004), but this variable was not significantly correlated with either the presence and number of fox scats, nor parasite prevalence and diversity, suggesting that the amount of greenspace is a better indicator of the modification of ecological processes that lead to changes in the infection dynamics of urban foxes. The positive correlation between greenspace ratio and parasite metrics was not found in the species-specific models run on parasite prevalence, which showed no single distinguishable pattern. I believe this is probably due to the fact that these models by design have a distribution that is more zero-inflated (and hence overdispersed; Czado *et al.*, 2007), making the identification of underlying patterns more difficult. For this reason, I believe that the community-wide models I presented above represent a more robust and reliable metrics of the impact of urbanisation on parasite infection dynamics in this system.

For logistic reasons, only public green spaces were surveyed, I do not have data regarding the use of private gardens by foxes in this study area, but previous studies have shown that private gardens represents an important source of anthropogenic food for foxes (Contesse *et al.*, 2004). The suitability of these sites 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; similarly Newman et al. (2003) found that 86% of denning sites were located in back gardens, although this figure dropped to 40% when the population density crashed following a mange outbreak (suggesting that this habitat is not the preferred one). On the other hand, in their study on urban foxes from Wroclaw, Duduś et al (2014) found that back gardens, despite being the most used habitat, were not a suitable habitat for natal dens. It is possible that foxes inhabiting private gardens behave differently since these denning sites are markedly smaller than the sites I investigated, but probably relatively undisturbed in comparison. I also do not have direct information regarding the foxes that deposed the faecal marking, which does not allow to make any kind of inference on the individual parasitological status; I assumed that marking from a single site were from a single fox group, given the territoriality of this species (Doncaster and Macdonald, 1991), but I could not distinguish between different individuals. Finally, as in every scat survey, morphological identification of samples in the field is not completely reliable (Davison *et al.*, 2002) and it is possible that some samples I assigned to foxes were from dogs, and vice-versa. This is a confounding factor I am aware of, but I deemed it relatively uninfluential in the overall analysis.

This study highlights the complexity of the interaction between urban environment, the foxes that live in it, and their parasites; my results showed that some characteristics of the urban environment such as the scarcity of green areas and the high level of landscape fragmentation have an impact on both the marking behaviour of foxes and parasite diversity and prevalence. Including fine scale landscape characteristics in this kind of studies is a vital step toward a better understanding of the underlying mechanisms driving infection dynamics in urban environments.

Chapter 4

A longitudinal investigation of temporal patterns of gastrointestinal parasite infection in urban red foxes from Edinburgh (UK)

Fox: One step at a time.
Mrs Fieldmouse: Some of us have bigger steps than others.
Adder: And sssome of us have no sssteps at all!

The animals of the farthing wood,
ep.10, “Between two evils”

4.1 Abstract

Seasonal variation in the host-parasite dynamics are often overlooked in disease ecology research, but they are of vital importance, especially in heterogeneous landscapes such as urban ones. Accounting for temporal patterns allows to identify the long-term effect of other variables, such as climate and nutrition, on the parasite community.

Here, I investigate the effect of microclimatic conditions (temperature and humidity) on the parasite diversity, prevalence and burden of urban foxes from Edinburgh. I longitudinally sampled six sites for a nine-month period and applied a multi-model approach in order to determine the best temporal pattern describing the parasite community.
I found that a structured, site-specific temporal effect was the best fit for most of the models, indicating that even at such small scale, each fox group inhabiting a site, had different dynamics, likely caused by the unique characteristics of the urban landscape surrounding each site. Furthermore, I found only a very small effect of temperature and humidity on parasite diversity, confirming that the warmer, more stable micro-climatic conditions of urban areas provide favourable conditions for soil-borne parasites.
Furthermore, a more natural diet (the presence of micromammals and rabbit specifically) was associated with a higher parasite diversity, suggesting that feeding on anthropogenic food sources could disrupt host-parasite dynamics.

4.2 Introduction

Infection dynamics are likely to vary in space and time, responding to a variety of factors, including environmental or host demographic variables. Epidemiological cross-sectional studies (i.e. studies conducted at a specific point in time, generally on multiple sites) can be useful to characterise the prevalence and diversity of parasite community in a certain host population (See for example Sato *et al.*, 1999; Di Cerbo *et al.*, 2008; Miterpáková *et al.*, 2009; Stien *et al.*, 2010), determine the relative abundance of a parasite species (König *et al.*, 2005; La Grange *et al.,* 2010; Shamsi *et al.*, 2017), or determine spatial patterns in the distribution of infection (Gortázar *et al.*, 1998; Guerra *et al.*, 2014; Tolnai *et al*., 2015). However, by design they are inadequate at capturing seasonal changes and temporal trends in parasite infection dynamics (Irvine, 2006).

While large-scale patterns in the seasonality of infections have been extensively investigated in the past, highlighting the role of latitude (Cook *et al.*, 1990) and altitude (Randolph *et al.*, 2000; Sándor *et al.*, 2017) in determining temporal infection dynamics, much less is known about the effects of small-scale variation in the temporal parasite dynamics.

Just as variation in urban landscape has the potential to disrupt the spatial dynamics in the parasite community (Liccioli et al., 2015; Gras et al., 2018), specific characteristics of the urban environment can disrupt temporal patterns of host-parasite dynamics (Bradley & Altizer, 2006). Gastrointestinal (GI) parasites are among the most common source of infections in wildlife (Brooker et al., 2006; Brooker, 2010), and urban red foxes are no exception. The GI parasite community of British red foxes have been extensively investigated (See Williams, 1976; Richards et al., 1993, 1995; Smith et al., 2003), and chapter 3 provides a detailed investigation of the GI parasite community of urban foxes in Edinburgh. While several environmental variables have the potential to have an effect on parasite dynamics, two factors have been hypothesised to be key for determining seasonal variability in GI parasite infection dynamics: (micro-) climatic conditions and host diet. Temperature (Haukisalmi & Henttonen, 1990) and humidity (Sissay et al., 2007) are the two main extrinsic climatic factors shown to impact the lifecycles and fitness of GI parasites. Both climatic variables impact the stability and duration of infectivity of the environmental form of the GI parasites, specifically the eggs, oocysts or free living larvae as the conditions of the soil have a deep effect on the viability (Weaver et al., 2010). The nutrition status of the host can also drive seasonal patterns of GI parasites (Holmes, 1993; Coop & Kyriazakis, 1999); starvation can exacerbate the effects of parasite infection, and annual cycles of food availability can impact parasite infection dynamics (Pedersen & Greives, 2008).

Urban environment can drastically alter both micro-climatic factors and host diet. The warmer, more stable climate of urban areas (a phenomenon known as “heat island”; Oke, 1973), can favour the persistence and development of soil-borne GI parasites in the environment (Weaver et al., 2010), increasing the infective pressure of these parasites. At the same time, the availability of abundant and reliable sources of food throughout the year, can prevent the cyclical nutrient deprivation of the hosts, allowing them to have better body condition and more resources to either mount effective immune response and/or be able to bear a heavier parasite burden (Cypher & Frost, 1999).

Despite the vast body of research on fox parasitology, studies focusing on the temporal patterns in GI parasite infections in this species are rare and very little is known about the seasonality of infection (Altizer *et al.*, 2006). Here I focus on the temporal patterns of parasite infection, trying to understand which variables affect infection dynamics of GI parasites of urban foxes in Edinburgh. In particular, I want to focus on small-scale heterogeneity in the temporal dynamics of fox parasite prevalence and burden within an urban context, and determine which variables are important in determining this variation. I will focus on two factors that are generally associated with GI parasite seasonal variability: (micro-) climatic conditions and host diet. In the previous chapter, I discussed the effects of spatial variation in the urban landscape and the effects that this variation has on the parasite community (see chapter 3). There I did not take into account the temporal aspect governing the host-parasites dynamics; in this chapter, I aim to determine whether there is a site-specific temporal pattern at such small scale by applying a multi-model approach (Brook & Bradshaw, 2006) in order to determine the best temporal structure for single parasite species prevalence and burden and parasite diversity. I combined field survey and modelling approach to determine i) if there is a temporal pattern in parasite dynamics and (ii) investigate micro-scale variation in the temporal dynamics of GI parasites across different sites. Most studies generally account for temporal variation by considering each temporal level (i.e. month, year, season) separately, as in a classic GLMM random effect (See for example Stieger *et al.*, 2002).However, this fails to capture the interdependence of temporal effects since consecutive levels are not independent (the values recorded in a month are dependent on the previous one). For this reason, smoothing algorithms (such as those used in GAMs) are generally preferable for modelling temporal trends (Zuur *et al.*, 2009). Smoothers can equip model timelines with more biological accuracy by “chaining” consecutive temporal levels that tend to vary together, while allowing a certain flexibility between levels (Brook & Bradshaw, 2006). Furthermore, this kind of temporal modelling can generally be easily integrated in spatiotemporal models, allowing for a more thorough account of spatio-temporal patterns. In this chapter I present an in-depth investigation of small-scale temporal variation in fox GI parasite dynamics by longitudinally surveying six sites within the Edinburgh urban area. I measured micro-climatic condition (temperature and humidity) at each site and recorded the consumption of certain food items and the diet diversity of the foxes in each site. I then tested the influence of these variables and tested different temporal structures to determine whether parasite dynamics follow a common temporal pattern or if there are site-specific dynamics.

Considering the nature of urban environment, where micro climatic conditions tend to be warmer and more stable (Shochat *et al.*, 2006), and the supply of anthropogenic food sources can sustain larger fox populations without cyclical crashes (Gloor *et al.*, 2001), I do not expect seasonal variations to be as important in this context; therefore parasite dynamics should remain largely stable throughout the course of the investigation.

4.3 Methods

4.3.1 Survey sites and design

In order to obtain longitudinal data on the GI parasites of urban foxes, I selected six sites across Edinburgh (Figure 4.1); a subset of those surveyed during the previous field season (see chapter 3).

This subset comprised those sites that yielded higher numbers of scats across the two previous surveying seasons, suggesting that they had a resident fox population. Each site was then surveyed every three weeks for fox scats in a period of ten months, between February and November 2018. The sites chosen were very different in size (varying from 0.11Km2 to 1.95 Km2), urbanity level (as defined in chapter 3), and level of anthropogenic

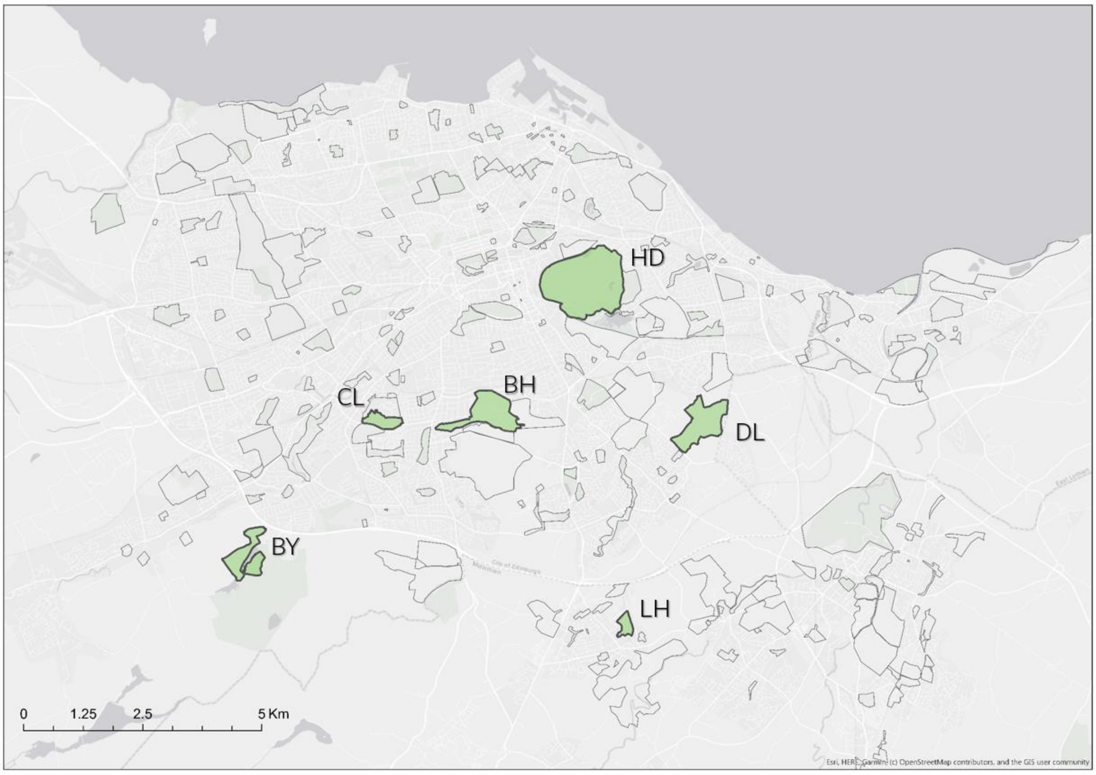

Figure 4.1 – Map of the six study sites (highlighted in green). The other green spaces in Edinburgh (which have been surveyed the previous year as part of the results presented in chapter 3) are represented by transparent shapes.

disturbance, since they included central city parks, as well as golf courses and nature reserves (Table 4.1).

SiteID	Site Name	Site type	Site Area	Transect length	Traffic Count	Road Cover	Population Density	Greenspace Ratio
BH	Blackford Hill	Semi Natural	0.684	4.072	0.080	0.785	55.060	0.732
BY	Bonaly	Natural	0.457	5.136	0.000	0.344	37.363	0.445
CL	Craiglockhart	Golf course	0.192	3.345	4.018	1.078	56.762	0.544
DL	Dardenall	Semi Natural	0.669	5.430	2.872	0.490	35.998	0.454
HD	Holyrood Park	Public park	1.948	6.915	1.192	0.541	42.664	0.866
LH	Loanhead	Public Park	0.110	0.149	1.911	0.777	51.291	0.272

Table 4.1 –Table reporting the details for each site surveyed: site area and transect length are expressed in Km^2 and Km, respectively. The classification of the site was done according to the greenspace dataset categories. The four urbanity measurements reported are calculated from an area including the actual site and a 300m planar buffer around it.

Sites were surveyed for fox scats along a transect, following a similar protocol presented in chapter 3. At each site, the transect was surveyed for fox scats every three weeks during a period of 10 months (February to November 2018), for a total of 13 consecutive sampling occasions (Figure 4.3). Whenever a fox scat was found, its location along the transect was recorded and, if and it was deemed fresh enough (not mouldy and still dark in colour), it was collected and brought to the lab for further dietary analysis.

Shortly after the start of this study, a construction site opened in one of the sites (DL), resulting in a significant reduction in the size of the site (roughly a quarter of the site was fenced up) and a shortening of the transect (part of which remained inaccessible for the duration of the study).

4.3.2 Gastrointestinal parasites and Diet analysis

Two types of analyses were conducted in each of the faecal samples: flotation analysis (to assess the presence and burden of gastrointestinal) and diet analysis (to determine which food items had been consumed and in which proportion).

For the flotation analysis, I weighed 3.5-7 grams of each faecal sample (roughly 25 - 50% of the sample, depending on the overall sample mass) and stored it in formalin (10% formaldehyde) and analysed using salt flotation and microscopy, in order to identify and count gastrointestinal parasites eggs/oocysts (see chapter 3 for details). For each sample I recorded the presence and burden (eggs/oocyst per gram) of each parasite species and calculated the parasite diversity index using the Shannon index.

The rest of each faecal sample was analysed using classical diet analysis techniques (Klare, Kamler *et al.*, 2011) to identify the food items consumed. The samples were stored at -80° C for at least a month before the analysis. Each sample was washed through a sieve of 0.5 mm mesh and food remains inspected. Mammalian hairs were identified to species level by microscopic examination of the cuticle pattern, medulla and cross-section (Figure 4.2) using two identification keys (Debrot *et al.*, 1982; Teerink, 1991). Undigested macroscopic remains were classified into broad food categories (fruit, invertebrates, birds, micro-mammals, meso-mammals, macro-mammals, and anthropogenic food). I recorded the relative proportion of these seven broad categories using a rough scale between 0 and 1 with0.05 increments. The diet data including the proportion of each food item was used to calculate the overall diet diversity per each scat, using the Shannon diversity index H (see chapter 3 for details).

The three mammal categories (micro-meso- and macro- mammals) were chosen to reflect different kinds of foraging behaviour. Micromammals included both micro-rodents such as mice and voles, as well as other small insectivores such as hedgehogs, moles and shrews. These species are smaller than foxes and provide an abundant but energetically expensive type of food because the energetic return on the hunting investment is relatively low. Mesomammals include mainly lagomorphs (rabbit and hare) which are closer in size to foxes and represent prey items with greater relative energetic return on hunting investment for foxes. (Glasser, 1982) Finally, macromammals include species that are generally too large for foxes to catch, except when the prey are at an extremely young age, such as deer (in this case mainly roe deer, *Capreolus capreolus*) or sheep (*Ovis aries*), but their carcasses can represent an abundant (albeit relatively rare) source of food that foxes can scavenge upon.

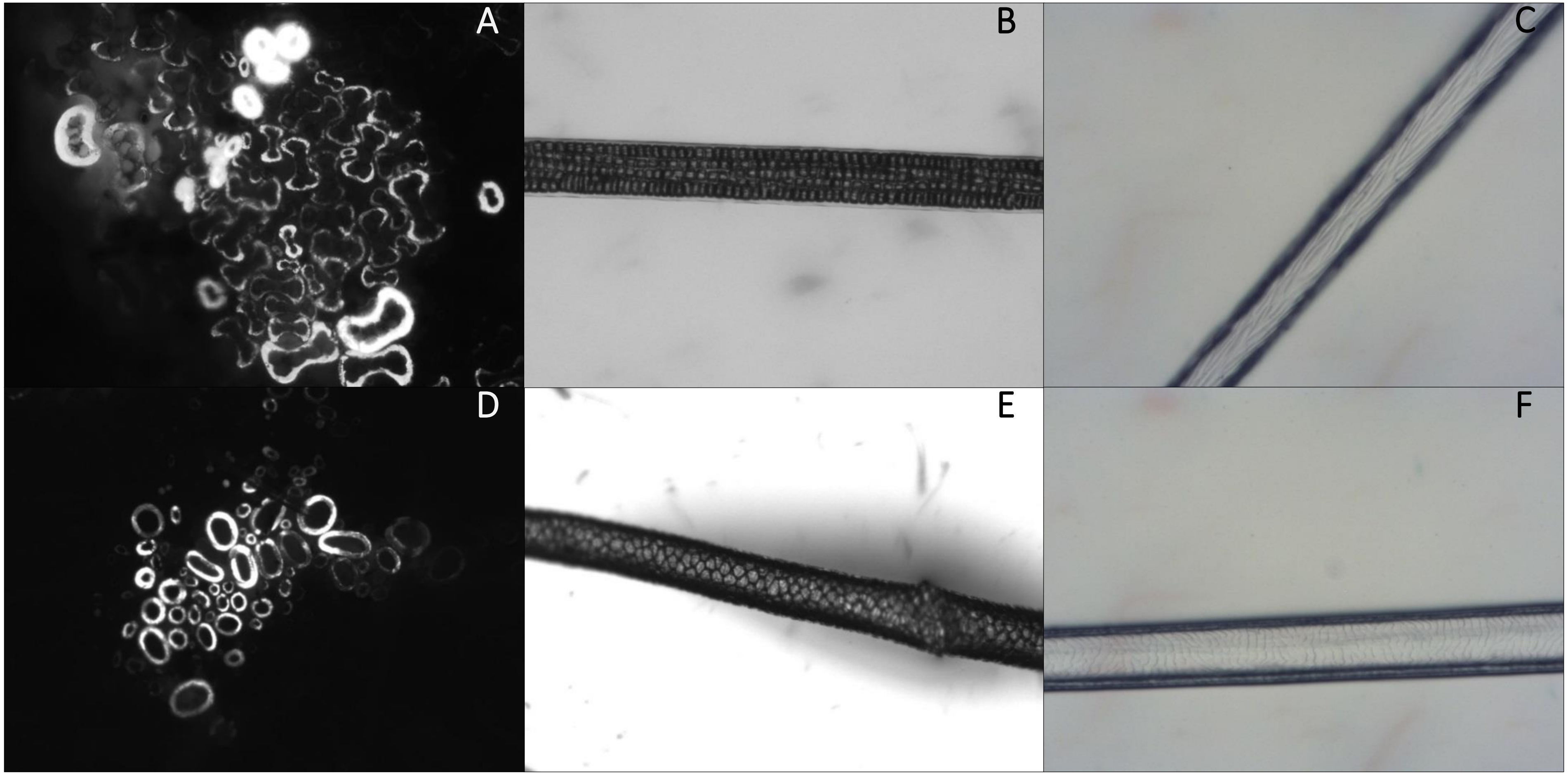

Figure 4.2 – Figure showing characterising features of hairs belonging to two different species: The European rabbit (Oryctolagus cuniculus, top) and the roe deer (Capreolus capreolus, bottom). The left images (A and D) show the cross-section of the hairs, the middle ones (B and E) show the medulla, while the right images (C and F) are pictures of the cuticle, obtained by imprinting the hair in transparent nail polish. Pictures curtesy of Hannah Romanowski.

4.3.3 Environmental variables

In order to obtain an accurate measurement of micro-climatic conditions, I deployed one data-logger in each site recording once per hour continuously for the entire duration of the survey period; five out of six were successfully recovered at the end of the survey. The data-logger from site BY was impossible to locate at the end of the study, hence, I used publicly available records of average temperature and humidity sourced from the Global Surface Summary of the Day (GSOD) dataset (http://www.ncdc.noaa.gov/) from the nearest station to this site. I extracted temperature and humidity data using the GSODR package (Sparks *et al.*, 2019).

4.3.4 Statistical analysis

4.3.4.1 Model structure

All the analysis were carried out in R studio using the package R – INLA (Lindgren and Rue, 2015). All the models were fit in a Bayesian framework using standard non-informative flat priors.

I fitted a series of mixed models to determine temporal dynamics of parasite diversity, calculated according to the Shannon index formula. The parasite diversity index is a continuous metric that contains only positive values, including zeros. However, given the high zero-inflation of this response variable, I decided to transform it in count data multiplying each value by 1000.

For each of the three most common parasite classes (*Uncinaria stenocephala*, *Euculeus aerophilus* and the coccidia genus), I fitted models to determine the effect of diet and climatic conditions on:

- Parasite prevalence: noted as a 1/0 value for each sample
- Parasite burden: noted as number of eggs/oocysts per gram of faecal sample

The parasite prevalence models were all fit with a binomial (Bernoulli) distribution; while for the burden models I tested three different distributions for each response (Poisson, negative binomial and zero-inflated negative binomial) in order to determine the best fit. All response variables for the parasite burden and the parasite diversity models were counts, and since some appeared to be zero-inflated, I tested three different distributions for each response: Poisson, negative binomial and zero-inflated negative binomial.

All models also included a series of linear predictors:

- Temperature, calculated as the average temperature of the three weeks preceding the survey date for each survey week, except for the first week, where the values are calculated for the previous week only (since the loggers were deployed 7 days before the first survey).
- Humidity, calculated in the same way as the temperature data.
- Diet variety, calculated using the Shannon diversity index for each scat.
- Presence/absence of three specific food items: fruit, rabbit and micromammals.

To account for differences in both fox and parasite dynamics between different sites I included site ID as a random effect in each model.

4.3.4.2 Temporal structure and model selection

In order to determine the best temporal structure for each response variable, I included a series of temporal predictors at increasing level of complexity (Table 4.2). The variable “Week” (with 13 levels, corresponding to each survey week) was modelled either as an unstructured or as a structured effect. Unstructured effects consider the variable as a categorical one, with each level being independently distributed; while structured effects model the variable levels (in this case consecutive weeks) considering the dependence of a level with the ones before and after it. In particular, I tested four different kinds of spatial effects:

- Independent and identically distributed effect (IID)

  This is analogous to a random effect in a standard GLMM, where each level is allowed to have an independent effect on the response variable

- Random walk of the first order (RW1)

  It defines an incremental change of the value recorded in the i_{th} week, in relationship with the previous one:

  $$x_i = x_i + \Delta x_i$$

  Where Δ_{xi} is normally distributed with mean 0 and variance τ^{-1}.

- Random walk of the second order (RW2)

  This takes into account both, the preceding $(i - 1)$ and following $(i + 1)$ time point, and results in a smoother function than rw1:

  $$\Delta^2_{xi} = (x_{i+1} - x_i) + (x_{i-1} - x_i)$$

  $$x_i = \frac{(x_{i-1} + x_{i+1})}{2} + \frac{(\Delta^2_{xi})}{2}$$

  Where Δ_{xi} follows similar restrictions than in the rw1.

- Autoregressive effect of the first order (AR1)

  This defines the value of the i_{th} observation as a function of the previous one, but introduces a noise term that allows more variability between consecutive time points:

  $$x_i = \rho x_i + \varepsilon_{ij}$$

  Where $|\rho| < 1$ and is normally distributed with mean 0 and variance τ^{-1}.

I applied these four temporal structures (iid, rw1, rw2 and ar1) to either the entire dataset or nested within the “Site” effect, effectively allowing each site to have its own temporal pattern. As a result, I fit eight models for each response variable and tested three different distributions (Poisson, negative binomial and zero-inflated negative binomial) for each count model. This rendered a total of 104 models tested, which were selected to find the best fit for each variable.

Model ID	Temporal effect structure
m1	Each week have an independent (IID) effect, common for the entire dataset
m2a	Structured temporal effect (RW1), common for the entire dataset
m2b	Structured temporal effect (RW2), common for the entire dataset
m2c	Structured temporal effect (AR1), common for the entire dataset
m3	Each week have an independent (IID) effect, which is site-specific
m4a	Structured temporal effect (RW1), which is site-specific
m4b	Structured temporal effect (RW2), which is site-specific
m4c	Structured temporal effect (AR1), which is site-specific

Table 4.2 – Table summarising the temporal structure of each model fit to test the best temporal structure for a determined response variable; the models are ordered by increasing level of complexity.

For the model selection, I used the Conditional Predictive Ordinate (CPO ; Geisser, 2017), to determine the best model fit for each response variable. CPO uses a leave-one-out cross-validation technique and it represents the probability of the observation y_i when the model is fit without that observation (Hooten *et al.*, 2015). In practice, the CPO algorithm detects surprising observations and determines the predictive power of the model. For each model, I calculated the $-\sum_{i=1}^{I} \log_e(CPO_i)$, that provides an overall measure of the model performance.

4.4 Results

4.4.1 Faecal samples

During the 13 weeks of survey, I found a total of 416 fox scats and collected 226 (54.3%) of them (Figure 4.3). The first two survey weeks yielded the highest number of scats, both found (165) and collected (86). From the 4th survey week onwards, the number of scats found stabilised at a much lower number. The survey scheduled on week 3 (early April) could not be carried out due to adverse weather conditions. Additionally, three wildfires in two survey sites (HD and BH) during August and September (FW08-11) forced the surveys to become more irregular. In these instances, I delayed the survey of all the sites in order to

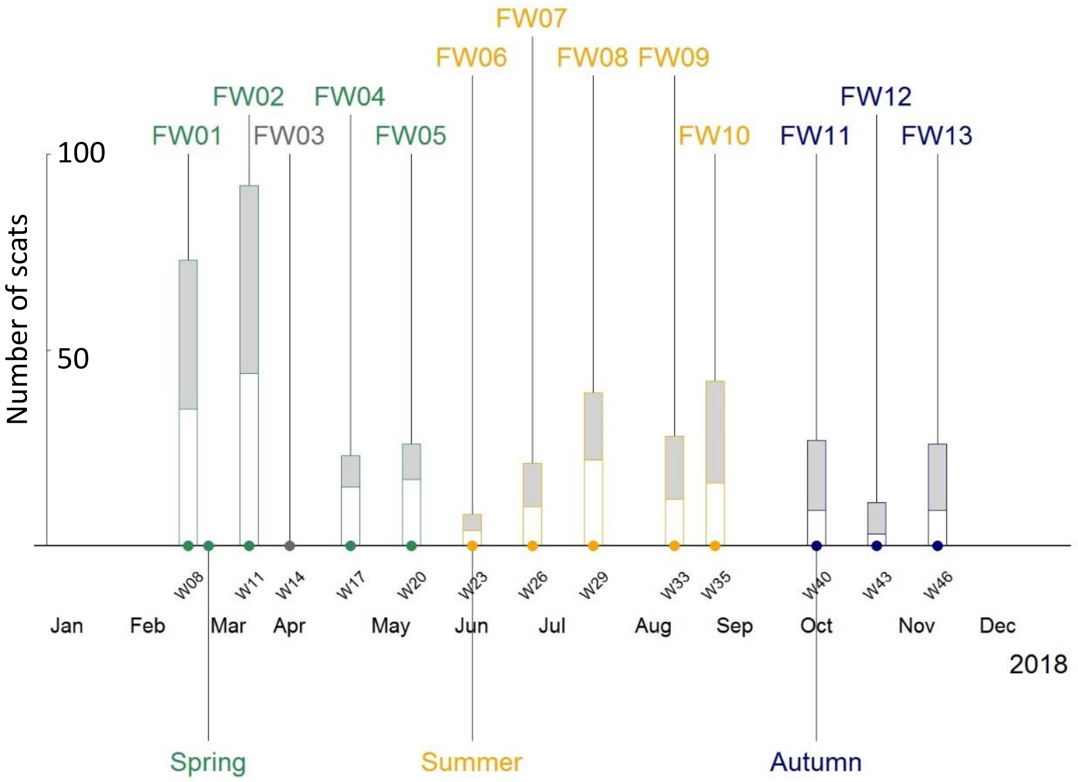

Figure 4.3 – timeline of the fieldwork conducted in 2018. Each survey week (labelled on the top of the timeline) are plotted against the month and week on the x-axis; weeks are calculated according to the ISO week date system, with the first week of every year starting on the first Monday in January (01/01 in 2018). The three survey seasons are also indicated (bottom of the figure). The number of scats found (full grey bars) and collected (white bars) are shown as a combined number form all the sites.

have a temporally consistent dataset, with all the sites being surveyed during the same week (Figure 4.3). As mentioned previously, it was only possible to recover 5 of the 6 data loggers deployed for each site. The average temperature, humidity and dew point calculated for each survey period can be found in Appendix 4.

The number of scats found in each site varied greatly (Table 4.3) with more than half of the total amount of samples (123/226) being from sites HD and DL. Larger sites with longer transects tend to have more scats, although the site that yielded the highest number of scats (DL) was not the largest, being about half the size of HD, which is the largest by far.

	FW	BH	BY	CL	DL	HD	LH
Spring	1	4(6)	10(17)	5(11)	9(15)	3(6)	7(18)
	2	4(8)	11(22)	7(12)	16(29)	7(14)	3(7)
	3	-	-	-	-	-	-
	4	0(2)	0(0)	0(0)	3(8)	8(13)	0(0)
	5	0(1)	1(1)	1(3)	1(4)	6(11)	2(6)
Summer	6	0(0)	0(0)	0(0)	0(0)	4(8)	0(0)
	7	2(2)	1(1)	0(0)	4(7)	4(10)	0(1)
	8	1(3)	2(3)	1(1)	4(10)	4(11)	6(11)
	9	4(9)	2(4)	3(4)	0(0)	7(11)	0(0)
Autumn	10	3(4)	3(4)	2(4)	14(23)	4(7)	0(0)
	11	2(3)	0(0)	0(0)	6(10)	9(12)	1(2)
	12	0(0)	4(4)	0(0)	4(7)	0(0)	0(0)
	13	8(10)	1(1)	1(2)	4(8)	2(4)	1(1)
Tot		28 (48)	35 (57)	20 (37)	65 (121)	58 (107)	20 (46)

Table 4.3 – Number of scats found (in brackets) and collected in each site for each survey week. The results from the third week are missing, as it was impossible to carry out the survey for logistic reasons. Survey weeks were spilt into three seasons of approximately 3 months each, roughly corresponding of Feb-May (spring), Jun-Aug (summer) and Sep-Nov (autumn).

4.4.2 Parasite community

All six taxa already described in Chapter 3 (*Toxocara canis, Eucoleus aerophilus, Uncinaria stenocephala; Taenia spp., Eimeria spp.* and *Isospora spp*, Figure 3.3), were also found in the samples collected for this analysis. The prevalence of each parasite taxon ranged between 8.4% for the *Taenia spp*, to 50.8% for *U. stenocephala*.

For the purpose of this analysis, I aggregated the two coccidian taxa (*Eimeria spp* and *Isospora spp*) given the difficulties in distinguishing the two taxa and because they have similar life cycles. Both prevalence and burden of the parasite taxa considered in the analysis varied considerably between sites (Table 4.4).

	BH	BY	CL	DL	HD	LH	Tot
U. stenocephala							
Burden	2.341	2.200	3.123	3.861	2.601	1.259	2.564
Prevalence	0.630	0.642	0.657	0.560	0.247	0.309	0.508
E. aerophilus							
Burden	0.249	1.351	0.543	0.232	0.331	0.061	0.461
Prevalence	0.354	0.492	0.380	0.222	0.280	0.240	0.328
Coccidia							
Burden	1.346	24.050	2.456	2.321	34.811	1.410	11.066
Prevalence	0.187	0.186	0.261	0.346	0.201	0.539	0.287

Table 4.4 – Table reporting the observed prevalence and burden for the three parasite species considered, presented for each of the six survey sites.

The prevalence of the single parasite species showed some temporal trends (Figure 4.4), with most parasites having a higher prevalence in colder months. In particular, most parasite taxa showed a lower prevalence (calculated as number of scats positive for a certain parasites over the total number of scats analysed) between week 6 and week 11, roughly corresponding to the summer period (between the beginning of June and the beginning of October). However it is important to remember that the number of scats found in a site would influence this representation (to a certain extent) since the prevalence of a parasite in a site where no scats were found would be zero by definition, and the number of scats found during the summer period was generally lower in all the sites (Figure 4.3).

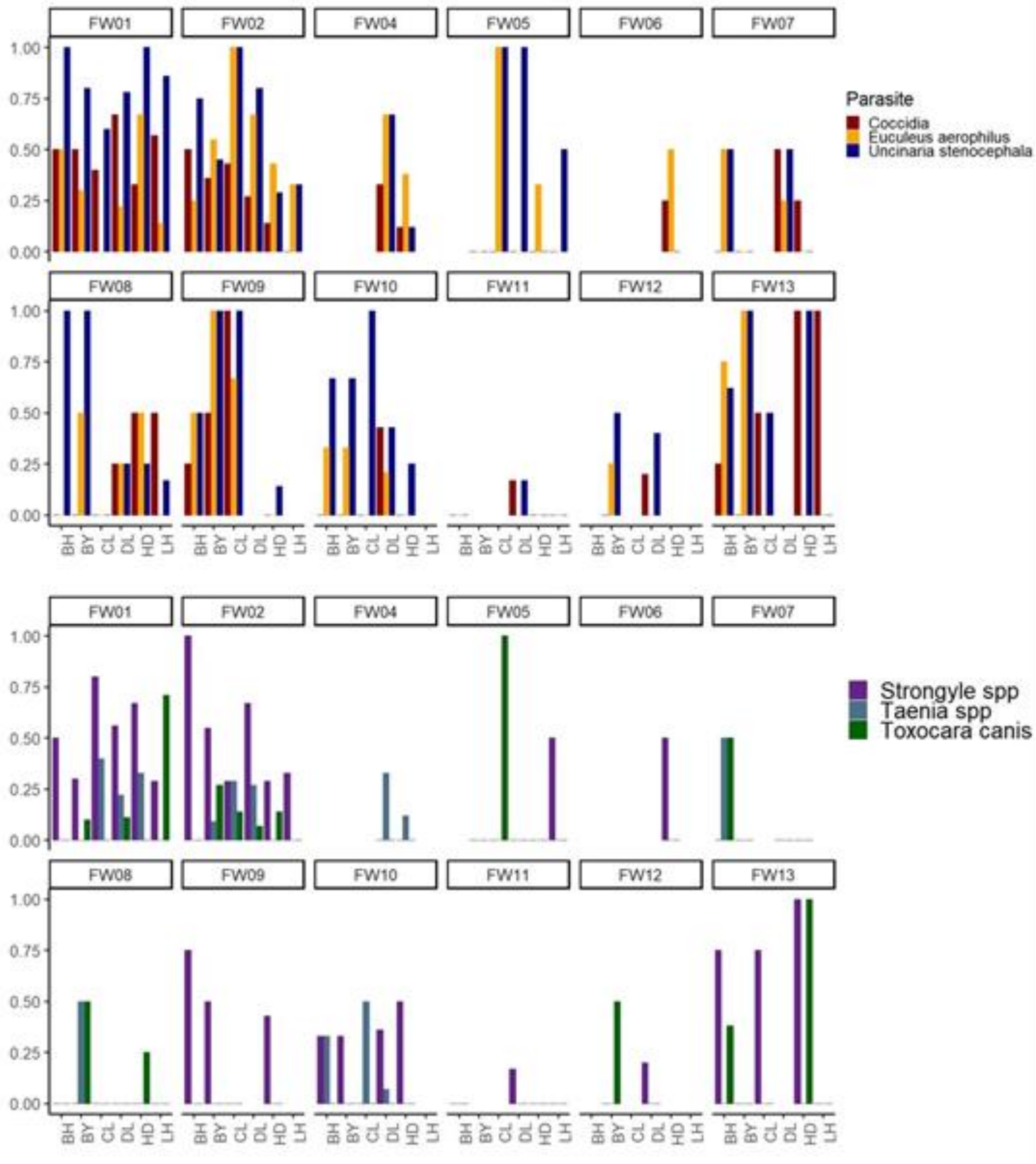

Figure 4.4 - Graphical representation of parasite prevalence for the six parasite taxa found during the longitudinal survey of fox scats. The taxa are divided in sets of threes in order to make the plot easier to read. The first three parasite taxa (coccidia, E. aerophilus and U. stenocephala) are the most represented in the dataset and were used in the longitudinal modelling. The other three taxa (Strongyle spp, Taenia spp and Toxocara canis) were rarer and the subset of data referring to these taxa is sparser. Both sets of parasites however show a possible temporal trend with lowest prevalence showed between week 6 and 11.

In addition to the parasite taxa described above, one sample found in DL contained the eggs of a *Mesocestoides* parasite (Figure 4.5). The egg clearly showed the parasite scolex, but exhibited two obvious differences from other Cestoda (mainly *Taenia* spp.) eggs I identified. Firstly, this egg was larger than a *Taenia*'s eggs, measuring about 40µm compared to ~25µm of *Taenia*'s eggs. Secondly, this egg was completely transparent, while *Taenia*'s eggs are brown. Considering that I only recovered this type of parasite in one sample, I cannot exclude the possibility that it might have been present in the fox digestive tract following ingestion of infected prey items. However, since mesocestoides are known parasites of carnivores, this seems unlikely.

Figure 4.5 – Picture of the parasite egg identified as a mesocestoides spp. The scolex is clearly visible and the transparency of the egg indicates this is not a Taenia spp egg. Furthermore, the measurements of the egg are consistent with a mesocestoides egg: both axis measured approximately 40µm. The picture was taken at a magnification of 40x.

4.4.3 Fox diet

The prevalence of the six food groups in the analysed scats varied greatly. Micro-mammals were the most commonly identified food group (52.9%), while fruit and meso-mammals were found in similarly lower proportions (30.8% and 30.4% respectively). Invertebrates were found in 24.2% of the scats, while macro-mammal remains and anthropogenic foods were relatively rare (12.8% and 8.8% respectively). From the three food items whose presence I recorded in all processed scats (micro-mammals, fruit and rabbit) only fruit prevalence showed a temporal pattern (Figure 4.6). The vast majority of fruit items were found in scats after the 7th week of survey

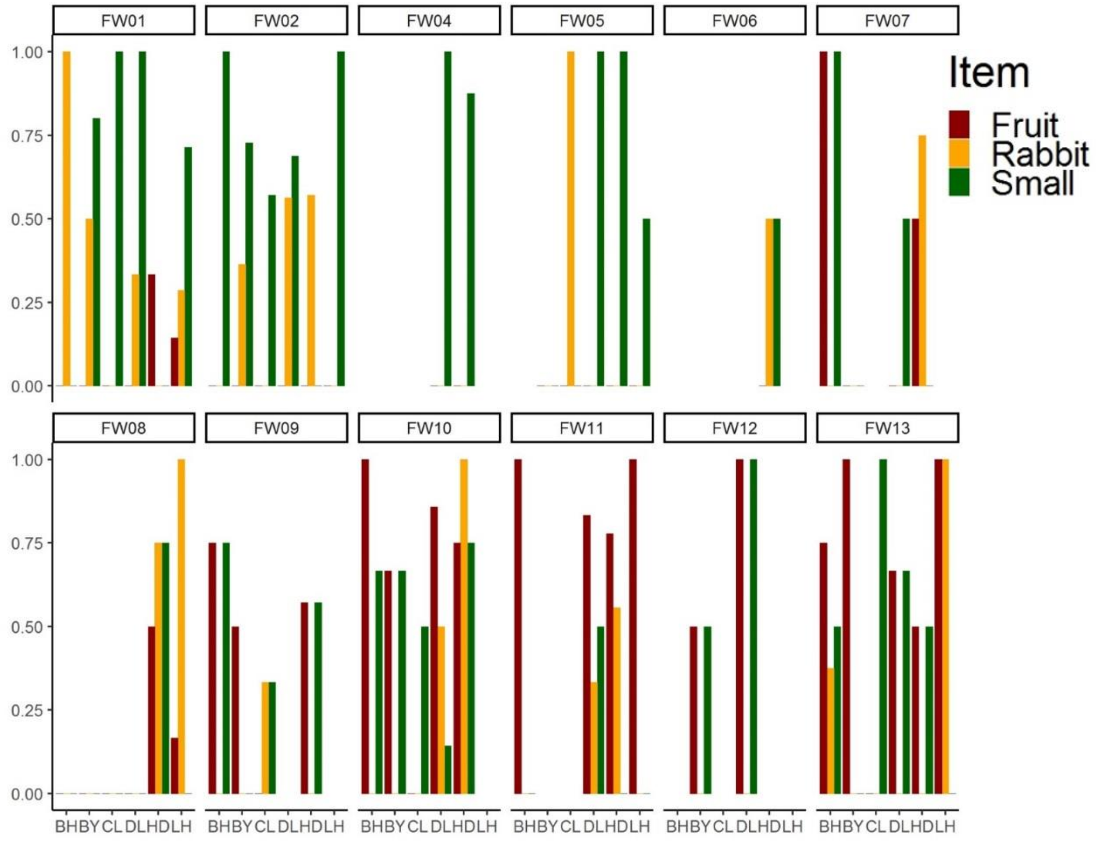

Figure 4.6 – Graph showing the proportion of scats found to contain the three food items considered (fruit, rabbit and small mammals), for each site in each survey week. The three food items considered are highlighted in different colour: fruit in red, rabbit in yellow and small mammals in green.

The average diet diversity scores calculated using the Shannon index showed site-specific differences in the diet diversity, with the largest site (HD) having the highest diversity score (average 0.79), whilst the smallest site (LH) had the lowest score (0.23). However, this does not imply a correlation between site size and diet diversity, since the second biggest site (DL) had the second lowest score (0.35)

The average diet diversity varied amongst sites; HD had the highest diversity overall, with an average of 0.79, while samples from LH had an average of 0.23. Diet diversity does not seem to vary throughout the seasons, as shown by the lack of any temporal trend in diet diversity (Figure 4.6). This suggests that the diet of urban foxes in Edinburgh not become more diverse in summer, when they have access to a wider variety of food items (such as fruits).

4.4.4 Model results

4.4.4.1 Model selection

Table 4.5 shows the CPO scores for all the models tested along with the failure score. For the parasite diversity model, the best fit was the zero-inflated negative binomial model with a site-specific temporal structure following a random walk 2 structure for the temporal effects (m4b).

The models fit on *U. stenocephala* and *E. aerophilus* (both prevalence and burden), followed the same temporal structure (a nested, structured temporal effect modelled as a RW2) and the distribution for the burden data was also zero-inflated negative binomial. On the other hand, the selected model for the coccidia burden (m4a) had a site-specific temporal structure modelled as a random walk of the first order (instead of RW2), and a zero-inflated negative binomial distribution. Finally, the best model for the coccidia prevalence had a completely unstructured temporal component (m1), with the "Week" term being modelled as an IID factor. Overall, the parasite models seem to have a well-defined, site-specific temporal structure, with coccidian being the only data deviating from this model structure.

	m1	m2a	m2b	m2c	m3	m4a	m4b	m4c
Parasite diversity								
Poisson	NA	NA	NA	NA	NA	NA	NA	NA
Neg Binomial	1002.442	1004.705	1074.915	1015.856	992.131	918.004	1005.853	1005.257
ZI Neg Binomial	792.308	792.324	793.291	792.371	792.365	798.933	**789.495**	792.346
U. stenocephala								
Poisson	NA	NA	NA	NA	NA	NA	NA	NA
Neg Binomial	1069.667	1069.049	1074.025	1079.572	753.34	497.144	**405.426**	686.204
ZI Neg Binomial	460.925	460.965	463.953	465.111	455.78	419.994	428.922	461.041
Binomial (prevalence)	141.034	141.045	138.569	133.333	137.47	133.801	**130.776**	131.13
E. aerophilus								
Poisson	NA	NA	NA	NA	NA	NA	NA	NA
Neg Binomial	159.034	159.047	159.778	159.041	159.031	157.839	**155.645**	159.054
ZI Neg Binomial	157.981	157.988	NA	NA	157.934	168.057	186.956	158.02
Binomial (prevalence)	94.989	94.991	95.979	94.987	94.986	95.018	**94.892**	94.985
Coccidia								
Poisson	NA	NA	NA	NA	NA	NA	NA	NA
Neg Binomial	434.603	435.031	517.461	463.91	412.056	342.895	585.606	435.028
ZI Neg Binomial	388.881	388.726	NA	392.634	366.033	**311.009**	517.19	389.063
Binomial (prevalence)	**104.01**	104.014	105.121	104.012	104.011	104.411	106.606	104.012

Table 4.5 – Table showing the CPO scores for each model fit to determine longitudinal patterns for i) parasite diversity, ii) Uncinaria stenocephala burden and prevalence, iii) Euculeus aerophilus burden and prevalence and iv) Coccidia burden and prevalence. The CPO failure rate for each model is colour-coded in red (min=0.009, max = 0.058); models with a failure score more than 0.1 (10%) were not considered and are indicated with NAs. Models with a lower score are considered to be a better fit, and the selected model for each response variable is highlighted in bold.

4.4.3.2 Model results

The results of the model fit to infer temporal patterns on the parasite diversity (Table 4.6) showed a significantly positive effect of both temperature and humidity, albeit with marginal size effects (0.051 and 0.016 respectively). Furthermore, the presence of rabbit and small rodents in the diet significantly increased the parasite diversity (0.506 and 0.475 respectively), and had a larger effect than temperature or humidity.

	Mean	SD	0.025q	0.975q
Intercept	**2.056**	**0.43**	**1.209**	**2.899**
Temperature	**0.051**	**0.021**	**0.011**	**0.092**
Humidity	**0.016**	**0.004**	**0.008**	**0.025**
Diet H Diversity	-0.244	0.19	-0.617	0.131
Fruit	-0.043	0.269	-0.578	0.479
Rabbit	**0.506**	**0.19**	**0.139**	**0.884**
Small	**0.475**	**0.183**	**0.118**	**0.836**

Table 4.6 – Table showing the results of the model fit to infer the effect of temperature, humidity and the four diet scores on the parasite diversity (calculated using the Shannon index) of fox scats collected from six sites across the urban area of Edinburgh.

However, neither fruit content nor the overall diet diversity index had an effect on parasite diversity (Table 4.6). 76% of the variance in the model was explained by the site-specific temporal term, while the sample ID term explained the remaining 24% of the total variation.

However, neither fruit content nor the overall diet diversity index had an effect on parasite diversity (Table 4.6). 76% of the variance in the model was explained by the site-specific temporal term, while the sample ID term explained the remaining 24% of the total

None of the covariates tested in the burden and prevalence models of the three parasite taxa, showed any significant effect of the variables included (Table 4.7), with the exception of a strong positive effect of rabbit presence on the prevalence of *Coccidia*. This indicates that fox consumption of rabbits increases their risk of acquiring coccidia, but does not affect the parasite burden (i.e. the number of coccidia oocysts). The temporal term (Site~Week) explained most of the *U. stenocephala* model variance (93.8%), while *E. aerophilus* showed a similar pattern than the parasite diversity model (the temporal term explained 65.8% of the variance, while sample ID accounted for the remaining 34.2%). Finally, for the coccidia burden model (fitted with a structured temporal effect using a site specific RW1), the temporal term explained 54% of the variance, while sample ID was responsible for the other 46%. The prevalence model variance was split evenly between the two random terms: week (50.3%) and site (49.7%; since this is a binomial model, the sample ID term was not included).

	Prevalence				Burden			
	Mean	SD	0.025q	0.975q	Mean	SD	0.025q	0.975q
U. stenocephala								
Intercept	0.119	0.44	-0.744	0.981	0.379	0.441	-0.487	1.245
Temperature	-0.042	0.032	-0.105	0.021	-0.038	0.033	-0.104	0.028
Humidity	0.001	0.005	-0.008	0.01	0.004	0.005	-0.006	0.013
Diet H Diversity	-0.386	0.337	-1.05	0.272	-0.197	0.331	-0.855	0.446
Fruit	0.149	0.408	-0.652	0.951	-0.27	0.395	-1.04	0.511
Rabbit	-0.362	0.342	-1.038	0.304	-0.47	0.358	-1.165	0.242
Small	-0.46	0.318	-1.087	0.16	-0.181	0.334	-0.838	0.475
E. aerophilus								
Intercept	-0.557	0.442	-1.425	0.311	-0.361	0.445	-1.234	0.511
Temperature	-0.002	0.034	-0.07	0.065	0.009	0.035	-0.06	0.078
Humidity	-0.006	0.005	-0.015	0.003	-0.004	0.005	-0.013	0.005
Diet H Diversity	-0.034	0.362	-0.747	0.674	0.218	0.376	-0.522	0.954
Fruit	-0.906	0.471	-1.843	0.007	-0.954	0.485	-1.906	0
Rabbit	0.237	0.375	-0.507	0.965	-0.062	0.404	-0.851	0.735
Small	0.144	0.35	-0.541	0.832	-0.061	0.364	-0.778	0.652
Coccidia								
Intercept	-2.121	2.175	-6.552	1.989	0.529	0.439	-0.334	1.389
Temperature	0.02	0.039	-0.057	0.097	0.056	0.03	-0.003	0.114
Humidity	-0.002	0.023	-0.045	0.045	0.004	0.005	-0.005	0.013
Diet H Diversity	-0.771	0.449	-1.685	0.078	-0.486	0.423	-1.297	0.362
Fruit	-0.54	0.507	-1.563	0.43	-0.37	0.491	-1.323	0.606
Rabbit	**1.573**	**0.418**	**0.77**	**2.408**	-0.346	0.428	-1.175	0.508
Small	0.784	0.459	-0.092	1.708	0.001	0.444	-0.872	0.871

Table 4.7 – Model results for the prevalence (left) and burden (right) models fitted on the three parasite taxa considered, significant effects are highlighted in bold. All models shared the same covariate structure.

4.5 Discussion

In this chapter, I investigated small-scale temporal dynamics of the parasite community of an urban fox population. I conducted a longitudinal survey of six urban sites in Edinburgh and measured the prevalence and burden of GI parasites in fox scats. I then modelled parasite diversity, prevalence and burden as a function of microclimatic conditions and fox diet in order to determine how these factors influence parasite temporal dynamics. I found evidence for small-scale variation in the temporal dynamics of parasite communities of urban foxes. Parasite diversity was positively associated with the presence of rabbit and other micromammals in the diet, indicating that a more natural diet could be associated with a more diverse parasite community. At the same time, I found a significant but weak positive association of parasite diversity with temperature and humidity. This could indicate that the stability of urban microclimatic conditions could dampen the strength seasonal changes in parasite diversity and reduce the influence of temperature and humidity.

At least for Edinburgh red foxes, a more structured temporal dynamic, modelled with a smoother, is a better option than modelling the temporal term as an independent, identically distributed (IID) variable (Schrödle & Held, 2011). A structured, site-specific effect was the best model fit to accurately describe parasite diversity, prevalence and burden of most species. The coccidia prevalence model was the only exception where the best model fit was one with a completely unstructured temporal effect. The temporal effect was site specific, indicating that each site had a different temporal dynamic. The fact that the site-specific temporal effect explained the majority of the variance in almost every model confirms that there is variation even at a small scale in parasite temporal dynamics. Furthermore, the sites considered in this survey were too far apart for foxes to habitually move between them (Marks & Bloomfield, 2006; White *et al*., 2016) so site variation can be considered as fox group variation (Iossa *et al.*, 2009). Considering the fragmentation of the urban landscape (Cadenasso *et al.*, 2007) and the effect that some elements of urban environments can have on the parasite community of urban foxes (e.g. greenspace; see chapter 3, but also Gras *et al.*, 2018), it is not surprising that small-scale changes in the surroundings of each site can also influence the temporal dynamics of fox parasites.

The only model where an unstructured temporal term was the one relative to coccidia prevalence; this could be explained by the fact that foxes can act as paratenic host for coccidia infection (i.e. “an organism that plays a role in a parasite's life cycle, as by harbouring its unhatched eggs, but in or on which no development of the parasite occurs”; Fayer, 1980). It is possible that the recorded coccidia presence in fox scats is the result of incidental ingestion of coccidia that are parasites of a prey species; furthermore, identifying different species of *Eimeria* (one of the two coccidia taxa present in this system) is particularly problematic using microscopy (Long & Joyner, 1984), which makes it difficult to detect paratenic coccidia through flotation analysis. The fact that coccidia prevalence is strongly positively associated with the presence of rabbit in the fox diet seems to confirm this hypothesis. This would also explain the lack of a structured temporal pattern in the model fitted on the coccidia prevalence data, while the burden model included a clear (although slightly simpler) structure in the temporal term. Burden measurements tend to be more robust to misidentification errors, since high numbers of coccidian parasites would be only found in scats infected by fox coccidian parasites, and hence the temporal pattern could not have been completely masked by misidentifications.

The results of the models showed drastically different patterns for model fitted on the diversity of parasite community, and the single species metrics. The Shannon index score for parasite diversity was influenced by a number of factors. Microclimatic variables such as temperature and humidity had a positive effect, as well as the presence of rabbit and micromammals in the diet; however, neither the presence of fruit in the diet, nor the diet diversity score had a significant effect on the diversity of the parasite community. On the other hand, none of the explanatory variables fitted in any of the single species models fitted had effect on the on parasite prevalence or burden of any given parasite species; with the exception of coccidia prevalence.

A more natural diet (less based on anthropogenic products) seems to be associated with a higher parasite diversity. This finding is in line with previous evidence suggesting that a diet based on anthropogenic food could reduce the diversity of parasite community in urban foxes (Deplazes *et al.*, 2004). However, in my models there was no direct correlation between consumption of anthropogenic food and parasite diversity, because the number of fox scats containing identifiable anthropogenic food remains was too low, and consequently could not be included in the statistical analysis. Only 12 out of 226 fox scats analysed contained anthropogenic food remains and this study has no evidence to claim a direct link between human food sources and parasite diversity. This might have been at least partially due to the limitations of using traditional diet analysis for the purpose of this study as this kind of analysis is notoriously unreliable, especially in estimating the amount of anthropogenic food consumed by carnivores (Fascione *et al*., 2004), given the complete digestibility of anthropogenic-sourced food, which means it usually undetectable by analysis of undigested remains. For this reason, newer technologies such as PCR-based methods could be more effective in identifying traces of anthropogenic food in the diet of urban carnivores (Symondson, 2002), as they would rely on the detection of DNA of species which are normally not available as a prey to wild carnivores. Furthermore, genetic screening such as qPCR might also be useful in characterising the parasite community of individual foxes (Mejia *et al.*, 2013), allowing a more precise estimation of parasite prevalence and burden.

Both temperature and humidity were found to have a positive, but very weak effect on parasite diversity, which was somewhat surprising giving the importance that environmental conditions play in the viability of the infective stage of many soil-borne parasites: warmer and wetter conditions allow parasite eggs/oocyst to persist for longer in the soil, increasing the infective pressure on resident foxes (Brooker et al., 2006). These results could potentially reflect the stability of the environment (Shochat *et al.*, 2006), where temperatures are never high or low enough to be detrimental to the viability of the eggs. However, it is important to remember that the data I collected only refer to sites within or around the urban area of Edinburgh, so it is not possible to draw a comparison between the effect of temperature and humidity in landscapes that experience more drastic swings. Furthermore, I lack the direct temperature and humidity measurements for the only sites that could be considered properly rural (BY), since I could not retrieve the data logger at the end of the survey and had to use weather data sourced from the GSOD website instead. For all these reasons, forming a direct link between the lack of effect of temperature and humidity and the parasite metrics on the base of my data is ultimately not possible.

These results show how parasite communities can respond to environmental factors, while single species show no temporal variation. Furthermore, a structured temporal effect was best at describing almost all the parasite dynamics measured. These results also highlight the importance of including a site-specific term in longitudinal studies including several sites, even when they are very close together, since I found stronger differences between sites than throughout time.

4.6 Acknowledgements

I would like to thank my Honours student, Hannah Romanowski for conducting the diet analysis and take the pictures of the hairs showed in figure 4.2. She has been an exemplary student and showed exceptional dedication for a truly ungrateful task.

Thanks a lot for all your help.

Chapter 5

Determining the impact of urbanisation on parasite infection of European red foxes: a large-scale, spatio-temporal meta-analysis.

Multa novit vulpes,
verum echinus unum magnum

Archilochus

5.1 Abstract

The presence of red foxes in urban environment is now a common occurrence in many European countries; urban environment deeply changes the behaviour and ecology of foxes, but it can also have indirect effects on their parasites.

Many studies have investigated the effect of urbanisation at a local scale, but efforts to produce a comprehensive analysis of the overall effect of urbanity level on the parasite prevalence of red foxes are lacking.

With the collaboration of 35 research groups from across Europe, I assembled a dataset of parasites and pathogens infection status of red foxes across 27 European countries and spanning 20 years. I used R-INLA to develop a spatio-temporal model to determine the effect of increasing levels of urbanisation on the probability of infection of wild red foxes; I found that microparasites respond strongly to urbanity, and their prevalence is highest at medium levels of urbanisation (~70% of built-up space).

This is the most comprehensive study on the effect of urbanisation on the disease ecology of foxes to date, and will help our understanding of the effect of urbanisation on the disease ecology of wildlife.

5.2 Introduction

The presence of wild red foxes in urban areas is a relatively recent phenomenon in Europe, but since it was first reported in London in the early 1900s (Teagle, 1967), it has steadily increased, becoming a common occurrence in many European cities (Gloor *et al.*, 2001). There have been concerns for the implication that the increased proximity of foxes would have on public health, since foxes can carry a multitude of parasite and pathogens, some of which can be transmitted to livestock, pets and even people (Gortázar *et al.*, 2007).

One of the consequences of this phenomenon is that the amount of research on urban foxes increased drastically; this includes many studies on fox behaviour (e.g. Iossa et al., 2008, 2009; Soulsbury et al., 2008, 2011) and ecology (e.g. Harris, 1981; Harris and Smith, 1987; Saunders et al., 1997), specifically in urban settings. Other studies focused on the effect that living in urban areas have on the disease ecology of foxes, and the effect that living in urban areas can have on parasite dynamics. The results of this kind of studies can be sometime contrasting (Reperant *et al.*, 2007a), even with the context of the same study system (Comte *et al.*, 2013); this is at least in part due to the heterogeneity of urban areas, and the difficulties to draw meaningful comparison between data sourced from different cities. For this reason, the results of this kind of studies, while valid for the specific study location, cannot be used to extrapolate general trends outside to the specific context of the study. Some attempts to draw generalised conclusions and infer the mechanisms behind the changes recorded in the parasite prevalence were made (see for example Deplazes et al., 2004; Liccioli et al., 2015); however, these conclusions are generally observational or in the form of opinion pieces.

In addition to this body of data, many large-scale programs exist across Europe, with the purpose of monitoring (e.g. Karamon et al., 2015), and in certain cases control (Smith and

Harris, 1989), the spread of zoonotic diseases in foxes, both from urban and rural settings. These tend to be technical reports of infection prevalence measured at a large scale (both spatially and temporally), generally as part of publicly funded schemes.

Despite the interest in the subject, and the great amount of work published, studies attempting to draw a synthesis of the data available and formally model the overall effect of urbanisation on fox parasite dynamics are rare; this is at least partially due to the difficulties of generating a meaningful synthesis of such diverse dataset, which are manifold: the most important one, is the lack of a unified definition of what constitute a urban environment (Weeks, 2010). The intrinsic heterogeneity of urban landscapes makes it particularly hard to generate a metric to accurately measure the urbanity levels (Hahs & McDonnell, 2006), and hence most studies only report values from contrasting environment (generally urban vs rural; Weeks et al., 2003). These categories are based on characteristics that are specific to the study system and meaningless for any other; however, in order to determine if there is an overall effect of urbanity on the parasite prevalence of foxes, it would be important to be have a unified metric, which could be applied to all the data.

Another problem, is the heterogeneity of the studies; a synthesis of the available data on urban fox parasitology will have to bring together studies on many different parasite species (some of which might have a different response to urbanisation levels), as well as vastly different methods used, both to collect the data and to detect parasite infection (Egger et al., 1997); this is a problem that makes particularly difficult to conduct a meta-analysis of observational studies, as opposed to randomised trials (Mueller *et al.*, 2018).

Finally, for large-scale datasets that are distributed over entire continents and span decades, the spatial and temporal autocorrelation terms need to be taken into account. Fitting models with an explicit spatial effect has historically been difficult due to computational limitations. Bayesian inference using MCMC methods have become very common in the past few decades to fit this kind of models, but they are computationally expensive and tend to require a long running time. this is a deterministic algorithm proposed by Rue et al (2009). Recently, the use of Integrated Nested Laplace Approximation (INLA) has emerged as a valid alternative to MCMC inference. INLA can provide accurate and fast results (Lindgren and Rue, 2015).

Here, I present a model designed to overcome these difficulties; rather than rely on published results I assembled a dataset by identifying relevant studies, and obtained the georeferenced raw data by contacting the authors directly.

In order to account for heterogeneity in the focus parasite species, some of which are phylogenetically very far apart, I characterised each parasite according to functional traits. These traits were chosen to reflect characteristics that have been previously been associated with differential prevalence between urban and rural settings.

The mode of transmission in particular has been previously linked to changes in parasite prevalence due to urbanisation; parasites that rely on intermediate hosts for transmission can show a reduction in prevalence in urban landscapes due to reduced predation on the intermediate host (Deplazes *et al.*, 2004). On the other hand, parasites that transmit through close-contact can exhibit a higher prevalence in urban areas due to high fox density (and hence higher contact rates between individuals; Devenish-Nelson et al., 2014). Certain characteristics of urban environments, such as landscape fragmentation, can disrupt the structure of arthropod communities and favour the aggregation of individual of a species that can act as a vector for certain parasites (Rizzoli *et al.*, 2014), increasing the infective pressure. Finally, the heat island found in cities (with a warmer, more stable microclimate; Shochat et al., 2006), can favour the persistence of resistance form of parasites in the soil (Weaver et al., 2010), translating in a higher prevalence of soil-borne parasites.

Another trait I took into account is the type of parasites, distinguishing between macro- and micro- parasites (Anderson & May, 1991); macroparasite infections tend to be chronic leading to morbidity rather than mortality, while microparasites reproduce exponentially in the host body leading to either death or immunity in a relatively short period of time (Hudson *et al.*, 2003). Foxes living in urban environments have been found to generally be in better shape than rural ones, due to their access to stable and abundant sources of food (Cypher & Frost, 1999). At the same time the stress of living in a highly disturbed environment can cause high level of glucocorticoids, which can inhibit the immune responses of urban foxes (Padgett & Glaser, 2003; Nelson et al., 2015). To account for the heterogeneity in the dataset I included detection methods and type of sample analysed as random effects, and used R-INLA to fit a hierarchical model with an explicit spatial and temporal autocorrelation term. Finally, I used two remote sensing datasets developed by NASA (https://sedac.ciesin.columbia.edu) to apply a common, unbiased measure of urbanity to the entire dataset, and determine whether there is an overall effect of urbanity level on fox parasite prevalence.

In addition, I also adapted the model structure to infer the effect of urbanisation on a subset of the full dataset to fit a model specifically on *E. multilocularis* data. This was done for two reasons; firstly, *Echinococcus multilocularis* represented the larger proportion of datapoints (16.3% of the entire dataset) and was hence most suited for a sub-analysis. Secondly, the vast amount of work specifically carried out on the effect of urbanisation on the prevalence of this parasite, makes it an ideal system to test the effectiveness of this model. This is the most comprehensive study on the effect of urbanisation on the disease ecology of foxes to date, and will help to bridge the gap between small-scale research and large-scale understanding of the underlying processes driving the effect of urbanisation on the disease ecology of wildlife.

5.3 Methods

5.3.1 Data collection

Since it is not standard practice to include point coordinates in published papers, my first step was to identify the existing body of work so I could contact the authors and source the raw data (including spatial references for individual datapoints).

I performed a search on Web of Science, using the same searching criteria used to construct the Global Mammal Parasite Database (GMPD; Stephens *et al.*, 2017). This is because I originally intended to use this database to identify relevant papers, but the section regarding carnivores was last updated in 2010 so I decided to expand the search using the same criteria.

The search string used was:

Vulpes vulpes **AND** parasite***** **OR** pathogen***** **OR** disease*****

In addition to this I also included a geographical restriction, as I only considered European countries (Russia was excluded from this definition for the purpose of this analysis); and a temporal one (1995-2018). I considered papers reporting the prevalence (presence/absence) of any “disease-causing organisms”, according to the GMPD definition (Stephens *et al.*, 2017). This include viruses, bacteria, protozoa, helminths, arthropods, and fungi. For convenience, I will refer to all these disease-causing organisms with the general term “parasite”. In order to exclude “case study” papers, I only considered studies with a sample size of at least 20 individuals. I manually screened the papers according to these criteria and were left with a total of 312 papers; a list of all the considered papers can be found in Appendix 5a.

After the selection process, I compiled a list of the papers satisfying the inclusion criteria and extracted the corresponding authors’ email addresses; I then emailed the individual authors.

I sent a total of 98 emails, trying to group together multiple papers coming from the same lab (i.e. sharing either the first or the last author), but this was not always possible especially for older studies. I requested details for the specific study cited as well as any other unpublished data collected by the researchers that would satisfy the inclusion criteria. Specifically, for each sample collected, I requested:

- Sample ID
- Spatio-temporal information (collection coordinates and date)
- Sample Type
- Host sex and age (if known)
- Parasite species
- Detection method
- Infection status (whether the sample tested was positive for the parasite)

The final dataset was comprised of 72914 datapoints from 17543 foxes, from 27 countries and included infection status for 67 parasite genera.

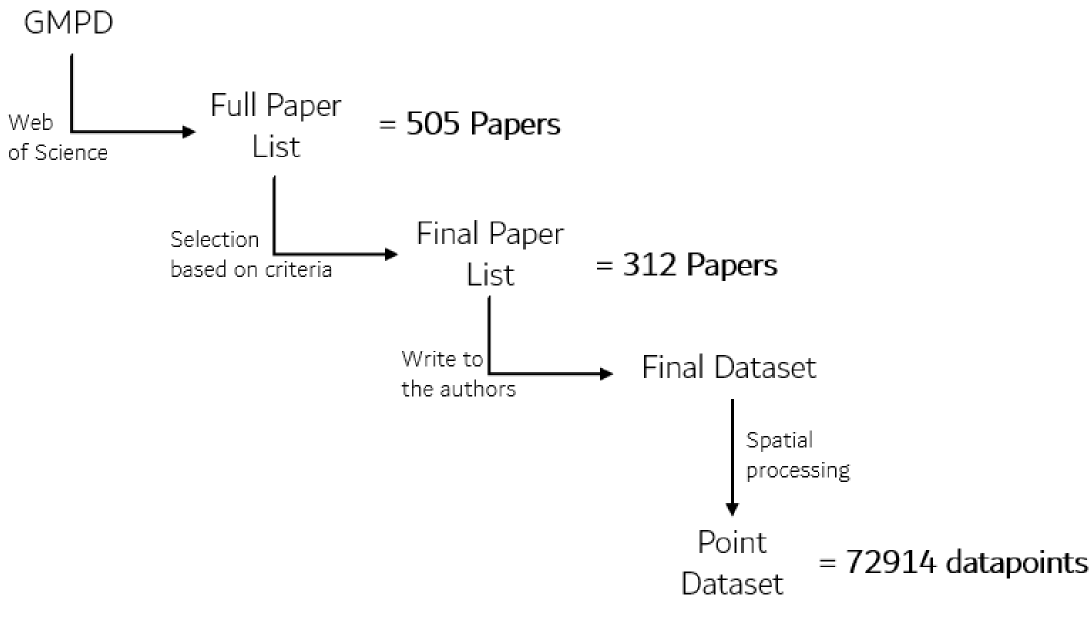

Figure 5.1 - Flow chart showing the data search, selection and processing, and the number of papers and datapoints retained at each consequent step.

5.3.2 Data processing

Not all of the returned data points were provided with a set of coordinates, a substantial proportion of data locations were given at a regional level (58.57%) or within a fixed radius from a specified centroid, the coordinates of which were provided (16.29%). Therefore, it was necessary to simulate the position of the points according to the information provided. Generally, if the precise coordinates of collection were not available, the authors provided either the coordinates of the nearest known point (along with an approximate distance from the collection point), or the name of the area where the sample was collected.

If the authors provided centroid coordinates and a radius, I simulated the point within this area, creating a circle of around the centroid with the given radius. If they provided the names of the administrative district where the sample was collected I used the Database of Global Administrative Areas (GADM; Global Administrative Areas, 2012) to match the name provided to the smallest possible administrative area and then simulate the point within this area (Figure 5.2). After this process, all the data points had a set of coordinates (Figure 5.3). I then modelled the probability of infection of foxes (as a 1/0 binomial response variable) as a function of a series of covariates, including an explicit spatiotemporal autocorrelation term, using the coordinates obtained via the simulation.

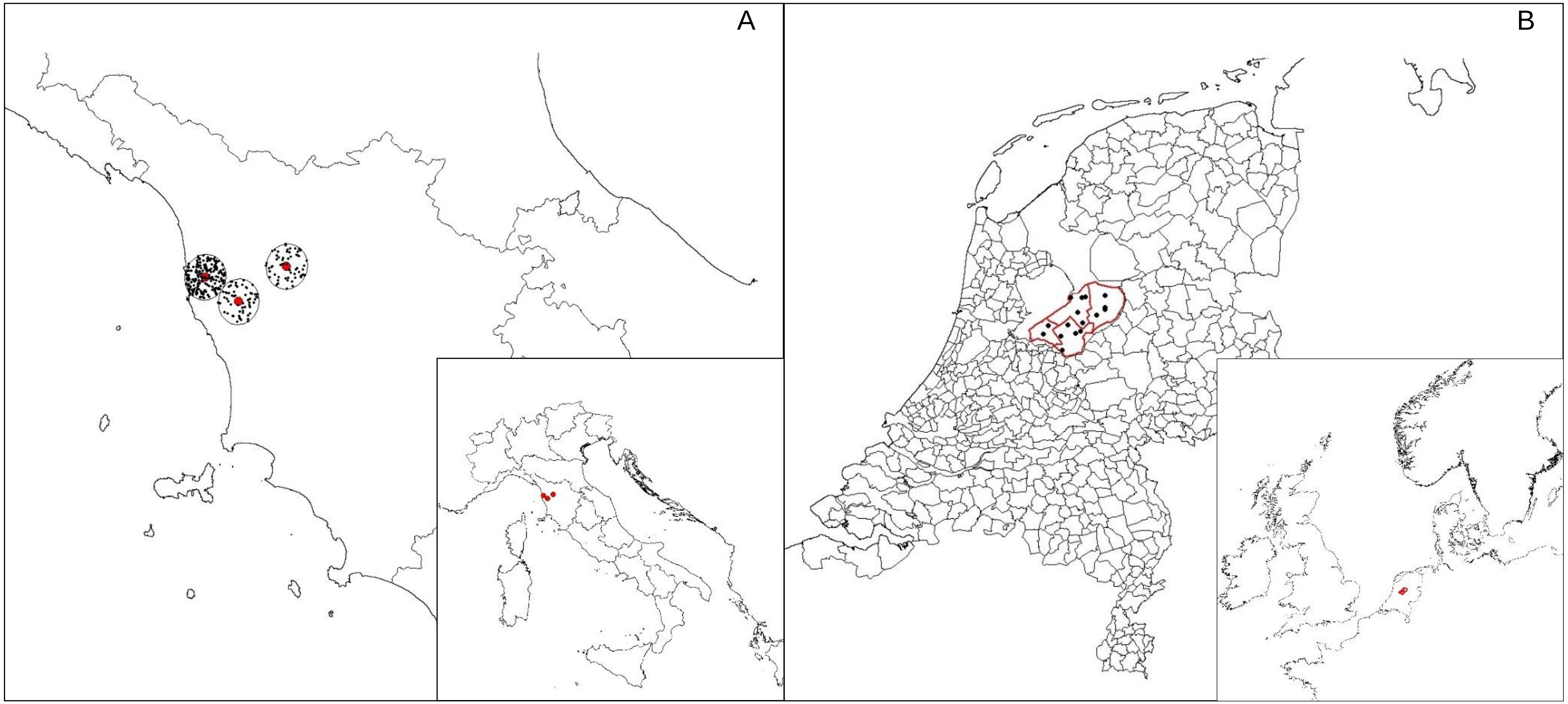

Figure 5.2 - Illustration of how point simulation works for a selection of points from two datasets (Van Der Giessen et al., 2004; Balboni et al., 2013). A) Some points were simulated in a given radius around a centroid, the coordinates of which were provided by the authors: this can be seen on the left, and the centroid points are shown in red, the figure shows the simulation area (with a radius of 10Km in this case). B) In other cases the authors only provided the name of the region where the sample was collected, and the points were simulated within the region (here shown in red), the name of the region was automatically matched to its extent using the GADM database.

5.3.3 Covariates

The covariates included in the model can be broadly classified in two categories: individual data, and environmental data.

Individual covariates are those intrinsic to the datapoints, irrespective of their geographical location. They were mainly provided by the authors and comprise:

- Host data (Sex/Age)
- Animal ID
- Sample type
- Parasite taxon (species, genus or family)
- Detection method

All were categorical, (see Appendix 5b for a list of all the levels for sample type, detection method and parasite taxa). Given the diversity in the parasite species included in the dataset, I decided to classify each taxon on the basis of functional traits. These traits considered the method of transmission (directly transmitted, indirectly transmitted, parasites that require one or more intermediate hosts and parasites that require a vector), and the type of parasite.

Each trait was then coded as a 1/0 for each parasite taxon and matched to the original data. Individual traits were not mutually exclusive, allowing for multiple methods of transmission. Table 5.1 shows the exact definition for each trait considered. The classification was done according to Soulsby (1982) and Taylor et al (2016), and if the two texts were not in accordance, I included both definitions.

For distinguishing between micro- and macro-parasites, I referred to the definition provided by Anderson and May (1991). The type of parasite is defined by its reproductive strategy: microparasite have direct reproduction potential and replicate within the host body, increasing their numbers, while macroparasites reproduce, generally producing eggs that are shed out of the body of the host to infect other individuals (but not increasing the parasite load of the current host). The full trait classification can be found in Appendix 5b. Environmental covariates were extracted from separate datasets according to the point geographical and temporal data provided. These comprise temperature and precipitation, as well as elevation and the urbanity level. Mean annual temperature (°C) and precipitation (mm/d) were obtained from the Global Surface Summary of the Day (GSOD) dataset (http://www.ncdc.noaa.gov/) from the nearest station to each point (within 50Km) for the year of interest; the extraction was done using the GSODR package (Sparks *et al.*, 2019).

Method of transmission	
Close	Parasites that are transferred by direct contact or require close proximity between infected and non-infected host.
NonClose	Parasites that have the potential to persist in the environment for a substantial amount of time, often in some sort of resistance form, before another host can pick them up
Intermediate	Parasites that require an intermediate host to transmit. Number of intermediate host (0, 1 or 2) and taxon of intermediate host were also recorded.
Vector	Parasites that require a vector to transmit. The Taxon of the vector was also recorded.
Type of parasite	
Microparasite	Parasite that replicates in the body of the host
Macroparasite	Parasite that reproduces in the body of the host

Tab 5.1 – List of the traits used to characterise each parasite taxa, along with the definition of each trait used for the classification.

In order to measure the level of urbanity at each point, I identified two datasets that measured different aspects associated with urbanisation:

- The global Human Built-up And Settlement Extent (HBASE; Wang *et al.*, 2017)
- Human Footprint (Venter *et al.*, 2016)

Both were downloaded from the Socioeconomic Data and Applications Data Center (SEDAC) website (https://sedac.ciesin.columbia.edu), which is one of the Distributed Active Archive Centers (DAACs) in the Earth Observing System Data and Information System (EOSDIS) of NASA. Figure 5.3 shows a map of the two overlaid dataset, along with the data points included in the analysis.

The global Human Built-up And Settlement Extent (HBASE) dataset is derived from the Global Land Survey (GLS) Landsat dataset, and it provides high spatial resolution (30mx30m) estimates of global urban extent for the year 2010. This is the most direct measurement of urbanity, specifically quantifying one of the most intuitive ways to identify urban areas: the amount of built-up space. The dataset provides a categorical (built-up/ not built-up) classification of each pixel, but I decided to download the dataset at a lower (~ 1Km) resolution in order to match the resolution of the Human Footprint dataset (see below); this resulted in a HBASE score between 0 and 100, according to the percentage of pixel scored as "built-up" per 1Kmx1Km cell.

The Human Footprint dataset was developed to provide a map of cumulative human pressure on the environment for the year 2009. It combines nine different measurements of human pressure, and it captures a more nuanced definition of urbanity, focusing more on the modification of landscape associated with urbanisation, such as the amount of roads and railways, or the extension of crop and farmland. This dataset has a lower spatial resolution of HBASE (1Kmx1Km) and varies between 0 and 50 (see Venter *et al.*, 2016 for details on how the score is calculated).

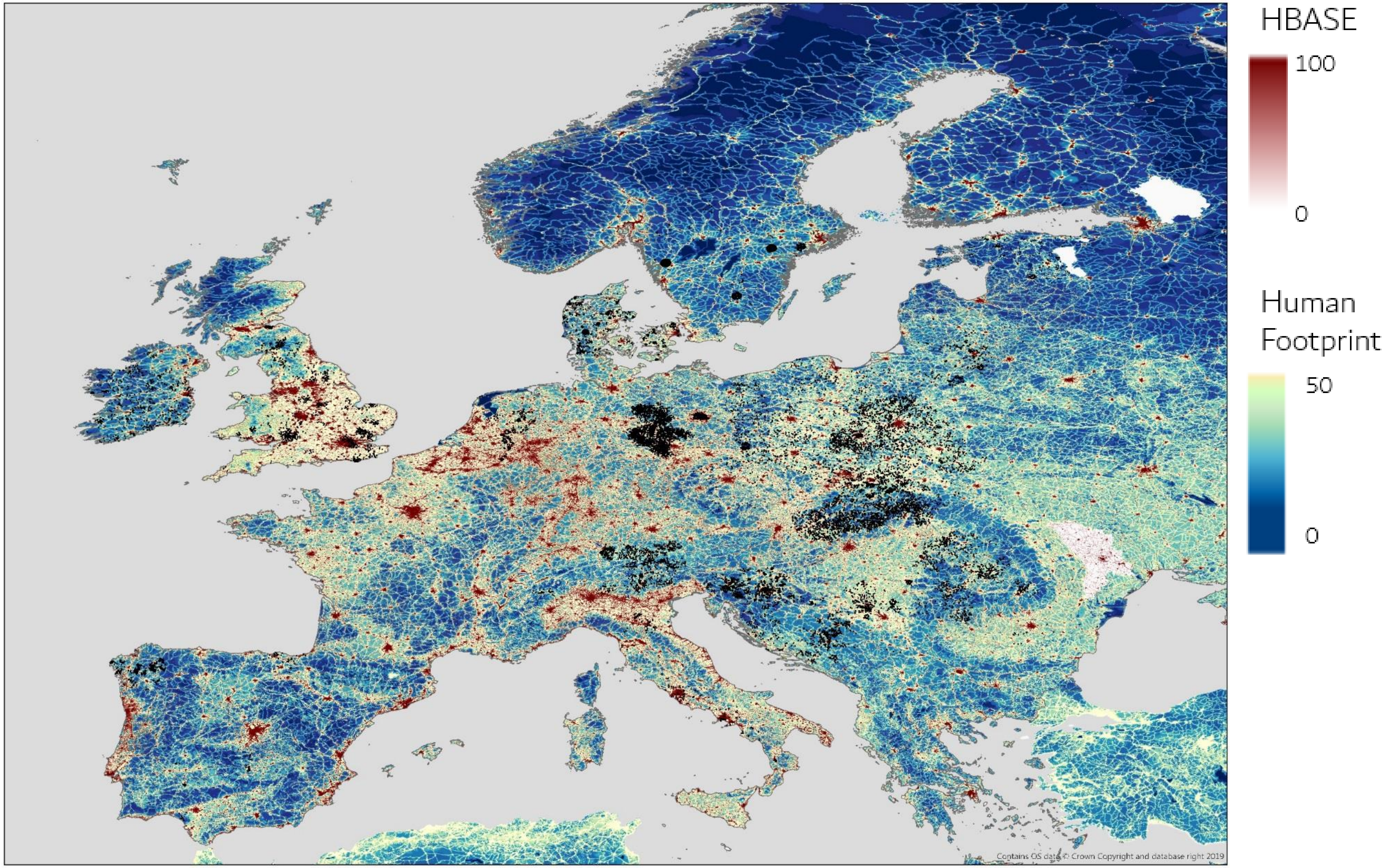

Figure 5.3 - Datapoints for the full model (black dots) plotted against the Footprint dataset (in yellow-to-blue) and the HBASE dataset (in red). The point locations were used to extract the corresponding values of Footprint and HBASE at each location.

5.3.4 Multi-parasite model

To investigate the variables affecting the infection status of foxes, I fitted a geostatistical model to the data, using the integrated nested Laplace approximation (INLA) approach, implemented in R using the R-INLA package (Lindgren and Rue, 2015). In brief, INLA uses several mathematical shortcuts to construct a discrete approximation of a continuous spatial process. This allows to fit complex model taking into account spatial autocorrelation in a computationally efficient way. The model assumes that the response variable values (in this case the infection status of the foxes modelled as a 1/0 response) are realisations of a continuous spatial process. This can be debated since the infection status of an individual does not actually happen outside of the individual itself (there is no infection possible where there are no foxes), however I deemed this classification appropriate because it reflects the geographical distribution of the parasites. Furthermore, the transmission process is a far more spatially smooth process (Graham *et al.*, 2004). To run the model, INLA initially generates a spatially discrete representation of the continuous data, using the finite elements approach (Lindgren & Rue, 2015). The mesh is effectively a net of triangles constructed around the data point locations so that the spatial autocorrelation element can be computed at the nodes of the mesh instead of being integrated over the entire space (which would effectively require computation at an infinite number of locations). In order to avoid boundary effects (increased uncertainty at the edge of the area), meshes tend to incorporate a smooth external boundary away from the area of interest consisting of a coarser mesh, in order to reduce computational cost (Lindgren and Rue, 2015). Sometimes, it is desirable to limit the extension of the mesh using a superimposed shape to “cut” the mesh. This is generally used in case of data that follow coastlines, since modelling the response variable beyond the coastline makes no biological sense.

Figure 5.4 shows the mesh used to fit the model. It was constructed using a non-convex hull around the area, setting a maximum triangle edge of 0.2 for the inner area and 1.5 for the outer one (all the values are expressed in the units used in the location input, in this case degrees). I decided not to use a coast boundary while constructing the mesh (see Appendix 5c for the mesh including coast boundaries); this is because there are areas in the mesh (namely in Denmark and across the Baltic sea) that are physically very close, but would have been completely separated by using a coastline (which does not allow for spatial autocorrelation between areas that are not physically contiguous). Hence, the mesh I constructed includes some portion of sea surface to account for the autocorrelation between these regions, but I will ignore the model results for these regions.

I used a cutoff value of 0.09, expressed in degree (which corresponds of roughly 9.9Km); this is effectively instructing the mesh to ignore locations of points closer than 10Km and consider them as a single point (for the purpose of constructing the mesh).

Once the mesh is constructed, it needs to be paired with the points' locations to create a projector matrix that effectively distributes the weight of each point between the nodes of the mesh depending on the proximity of the point to each node. Finally, INLA uses the SPDE (stochastic partial differential equation) approach to calculate the precision matrix for the gaussian Markov random field (Lindgren & Rue, 2011). This is what will be incorporated in the final model to account for the spatial autocorrelation between points. I incorporated PC (penalised complexity) priors according to Fuglstad *et al.* (2019) which penalise more complex models, shrinking them to the base one (one with no spatial autocorrelation term), unless there is significant evidence to support a spatially explicit model (Fuglstad *et al.*, 2019).

The model was structured using a spatially explicit hierarchical framework, which is similar to a GLMM, including both fixed and random effects. The response variable (fox infection status) follows a Bernoulli distribution (a binomial distribution with values of only 1 and 0).

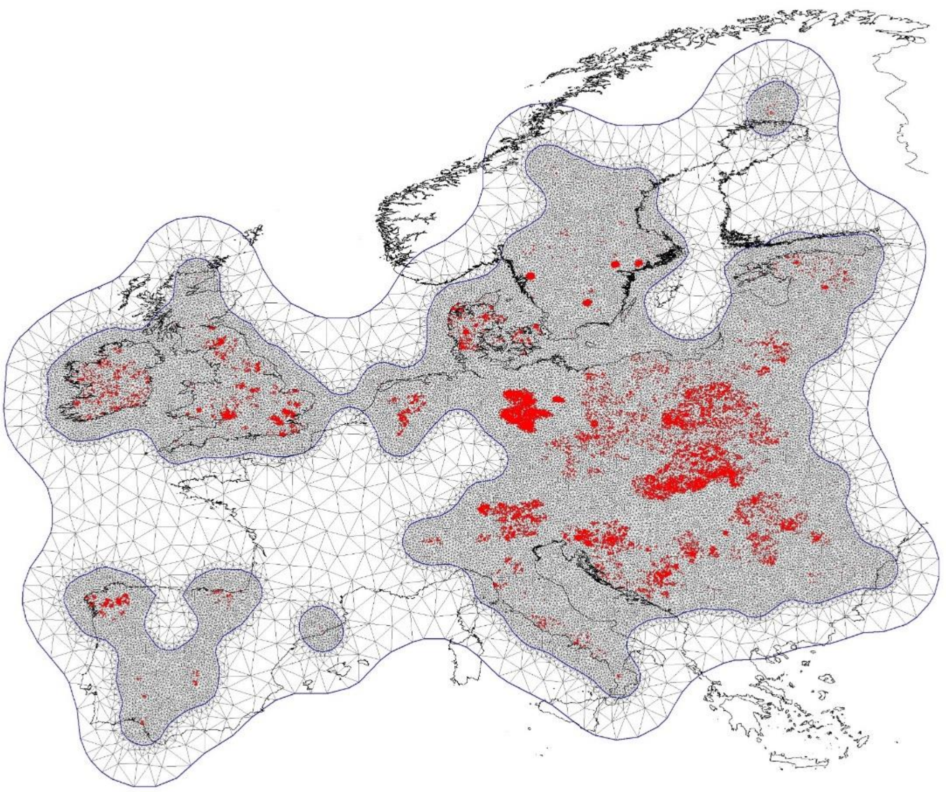

Figure 5.4 - The final mesh constructed to fit the full model (including all the parasite species); the red dots represents the datapoints' locations and the coastline of Europe has been plotted for reference. The mesh has 33337 nodes

The parameters were linked to an additive linear predictor η through a logit link function.

The structure for the linear predictor is defined as follow:

$$\eta = \beta_0 + \sum_{l=1}^{L} \beta_l x_{i(s)} + \sum_{k=1}^{K} f_k(\beta_s) W_k + \sum_{r=1}^{R} \gamma_r x_i + \xi_s + \varepsilon$$

Where $\beta 0$ is the intercept, βl defines the slope for the l^{th} linear predictor defined in space (and time) for each point $x_{i(s)}$; γ_r represents the independent and identically distributed (iid) random effects, and the function f_k defines the smoother for the nonlinear β_s predictors, where the regression coefficient vary with the predictor's level W_k. Finally ξ_s represents the spatial autocorrelation term (modelled using the spde level described above), and ε is the residual error variance.

In practice, the model contains nine linear fixed effects (Table 5.2, row 1-9), including both continuous and categorical variables. These include the spatial covariates (latitude, temperature, HBASE and Human footprint), as well as individual ones (parasite transmission traits and parasite type). The interaction between the urbanity predictor (HBASE in this case) and the parasite traits were modelled using a random walk of the second order (rw2), this was done in order to capture possible non-linear effect of the urbanity level on the different parasite traits (Table 5.2, row 10-14). I also included five random effects in the model, to control for animal ID, sample type, parasite genus and detection method (Table 5.2, rows 17-20). Finally, the model included a spatial effect (fitted using a spde model) and a temporal effect of year (modelled using a random walk of the first order, rw1), with no interaction between the two. The optimal spatiotemporal effect was determined using the Conditional Predictive Ordinates (CPO) on a series of partial models fitted using 10% of the dataset (Held *et al.*, 2010). I did not include all the covariates I collected in the model: the average yearly precipitation and elevation were excluded after performing a variance inflation factor (VIF) test to test for autocorrelation (I used a cutoff level of 2; Craney & Surles, 2002); host sex and age were also excluded from the model since only about 30% of the dataset included that information. Finally, I used the default flat priors for the model (mean 0 and precision 10^{-5}) as I wanted the results of the model to be solely informed by the data.

	Variable	Effect	Description
1	Latitude	linear	Continuous variable
2	Temperature	linear	Continuous variable
3	HBASE	linear	Continuous variable
4	Human Footprint	linear	Continuous variable
5	Close	linear	Categorical variable (0/1)
6	NonClose	linear	Categorical variable (0/1)
7	Intermediate	linear	Categorical variable (0/1)
8	Vector	linear	Categorical variable (0/1)
9	Micro	linear	Categorical variable (0/1)
10	HBASE X Close	rw2	Semicontinuous variable: NA when Close=0, HBASE otherwise
11	HBASE X NonClose	rw2	Semicontinuous variable: NA when NonClose=0, HBASE otherwise
12	HBASE X Intermediate	rw2	Semicontinuous variable: NA when Intermediate=0, HBASE otherwise
13	HBASE X Vector	rw2	Semicontinuous variable: NA when Vector=0, HBASE otherwise
14	HBASE X Micro	rw2	Semicontinuous variable: NA when Micro = 0, HBASE otherwise
15	Spatial Effect	spde	2D continuous variable
16	Temporal effect (Year)	rw1	Ordinal variable
17	Fox ID	iid	Categorical variable
18	Sample Type	Iid	Categorical variable
19	Parasite Genus	iid	Categorical variable
20	Detection method	iid	Categorical variable, NEC set to NA

Tab 5.2 - List of the predictors included in the full model (including all parasite taxa). The table also shows the type of variable, along with the type of effect used to model them.

5.3.5 Echinococcus multilocularis model

I also analysed a subset of data regarding the probability of infection of a single parasite species: the tapeworm *Echinococcus multilocularis.* This represented the most common parasite in the full datasets, comprising 11879 samples from 11388 individual foxes. Of these, 1957 (16.48%) were given exact locations, while 4336 (36.50%) were simulated at an administrative district level and 5586 (47.02%) at area level with centroid coordinates provided district (see above for details regarding the simulation process, Figure 5.2).

In order to account for the uncertainty in the point location, I decided to “split” each simulated point, further simulating a point for each 30Km^2 of the area according to the author’s instruction, using the same process described above. I then re-extracted the HBASE

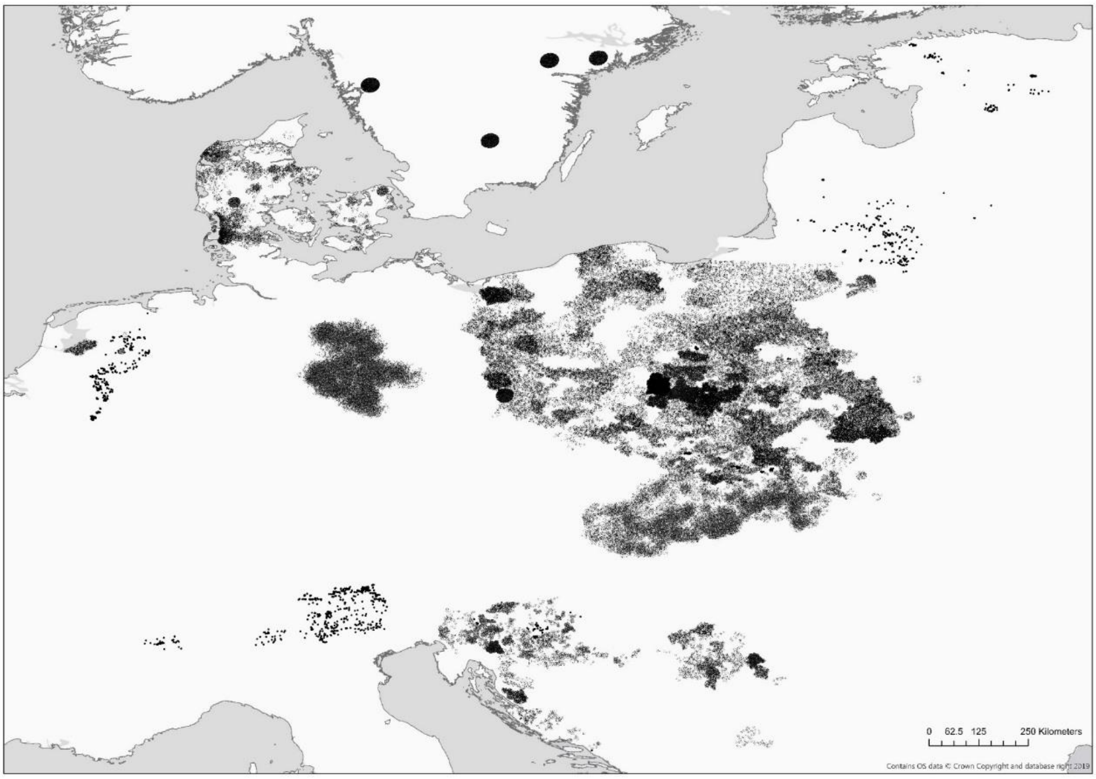

Figure 5.5 - Map showing the new dataset obtained for the E. multilocularis model. The transparency of the points is directly proportional to their weight (between 0.01 and 1)

percentage, human footprint level, temperature and latitude values for each of these points, while retaining all the data pertaining to the original point (ID, detection method and infectious status).

Through this process, I obtained *n* points per originally simulated point (n being directly proportional to the area of original point simulation). I then assigned a weight value to each of these points equal to 1/*n*, which would be included in the model, effectively sharing the log-likelihood of each point around the area of uncertainty (Figure 5.5). For computational reasons, I limited the number of simulated points to a maximum of 100 per original point.

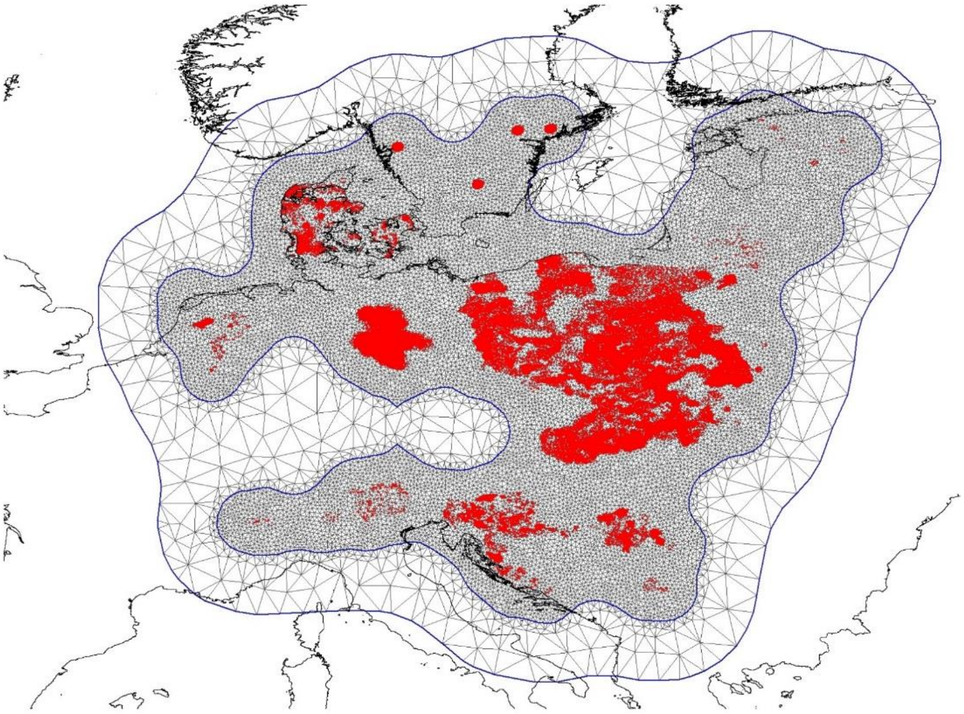

Figure 5.6 - The mesh used for the E. multilocularis model, plotted against the data points location (in red) and the Europe coastline (in black). The mesh had 16818 nodes.

This did not affect the points that had a precise location attached as they had a weight of 1 and hence were treated like standard data points. As a result of this process, the sample size increased from 12333 to 155276 datapoints.

Variable	Effect	Description
Latitude	linear	Continuous variable
Temperature	linear	Continuous variable
HBASE	rw2	Continuous variable
Human Footprint	rw2	Continuous variable
Spatial Effect	spde	2D continuous variable
Temporal effect (Year)	rw1	Ordinal variable
Fox ID	iid	Categorical variable
Sample Type	iid	Categorical variable
Detection method	iid	Categorical variable

Table 5.3 – List of the variables included in the E.multilocularis model, along with the type of variable and the effect used

The mesh for the *E. multilocularis* model was obtained with the same mesh parameters previously presented for the full model, but had a different extension given by the different location of the points; this resulted in a mesh of 16818 nodes (Figure 5.6). Similarly, PC (penalised complexity) priors were used for the specification of the spde model. The model structure was similar to the one presented for the full model, but did not include the parasite traits factors (Close, NonClose, Intermediate, Vector and parasite type), or the parasite genus random effect since this model is only about one parasite species. It also included both the HBASE and Human Footprint scores modelled with an rw2 structure. The full list of the effects included in the model can be found in table 5.3.

5.4 Results

5.4.1 Multi-parasite model

5.4.1.1 Linear Effects

Among the variables that were modelled linearly (latitude, temperature, HBASE score, Footprint score, and the five parasite traits: close, non-close, intermediate, vector and micro), only two showed a significant effect.

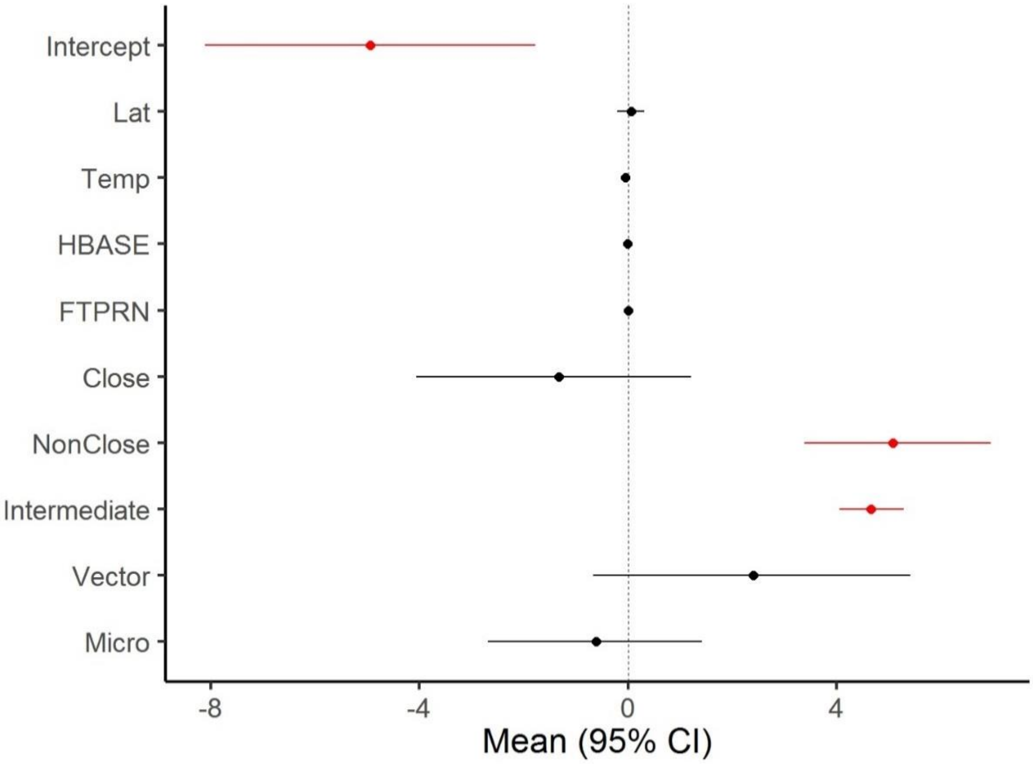

Figure 5.7 – Figure showing the individual effect of the variables modelled linearly, along with the 95% credible intervals. The red dots and line represent significant effects. The effects are shown in the linear scale (the model uses a logit link).

Non-closely transmitted parasites and parasites that require an intermediate host showed were both positively correlated with the probability of infection in foxes (figure 5.7); this indicates that the prevalence of this kind of parasites is higher than average. In other words, foxes are more likely to be infected by these kinds of parasites.

5.4.1.2 Non-Linear Effects

The three non-linear effect that explained the most amount of variation (Table 5.4) were sample type, parasite genus and detection method used (which explained 28.9%, 32.5% and 32.4% of the variation respectively). Spatial and temporal, and individual effects account for most of the remaining variation (4.1%, 1.1% and 1% respectively).

Component	Variance Explained	Proportion (%)
Range for spatial field	0.258	0.5
SD for spatial field	0.857	1.6
HBASE : Close	1.83E-05	<0.1
HBASE : NonClose	1.83E-05	<0.1
HBASE : Intermediate	9.94E-05	<0.1
HBASE : Vector	5.87E-05	<0.1
HBASE : Micro	6.58E-05	<0.1
Year	0.061	0.1
Fox ID	0.074	0.1
Sample Type	25.104	40
Parasite Genus	11.86	21.3
Detection Method	23.28	36.4

Table 5.4 – Table showing the variance explained by each non-linear effect included in the model, along with the corresponding proportion of variance explained by each component.

The effects for the individual levels of these variables can be found in Appendix 5d. The five interaction effects explained the least amount of variation (each less than 0.1% of the total variance) among the variables considered.

The parasite transmission traits (close, non-close, intermediate and vector), did not show any obvious pattern and the effect of different HBASE levels was generally not significant.

In contrast, the effect of HBASE score on microparasite infection probability followed a well-defined structure; the prevalence of microparasite infections is lowest at low-levels of

HBASE, and it increases steadily, peaking at medium-high levels of HBASE (~70%), and decreases again at higher percentages of built-up spaces. Overall, 73 out of 101 HBASE levels have a significant effect on the response variables (Figure 5.8).

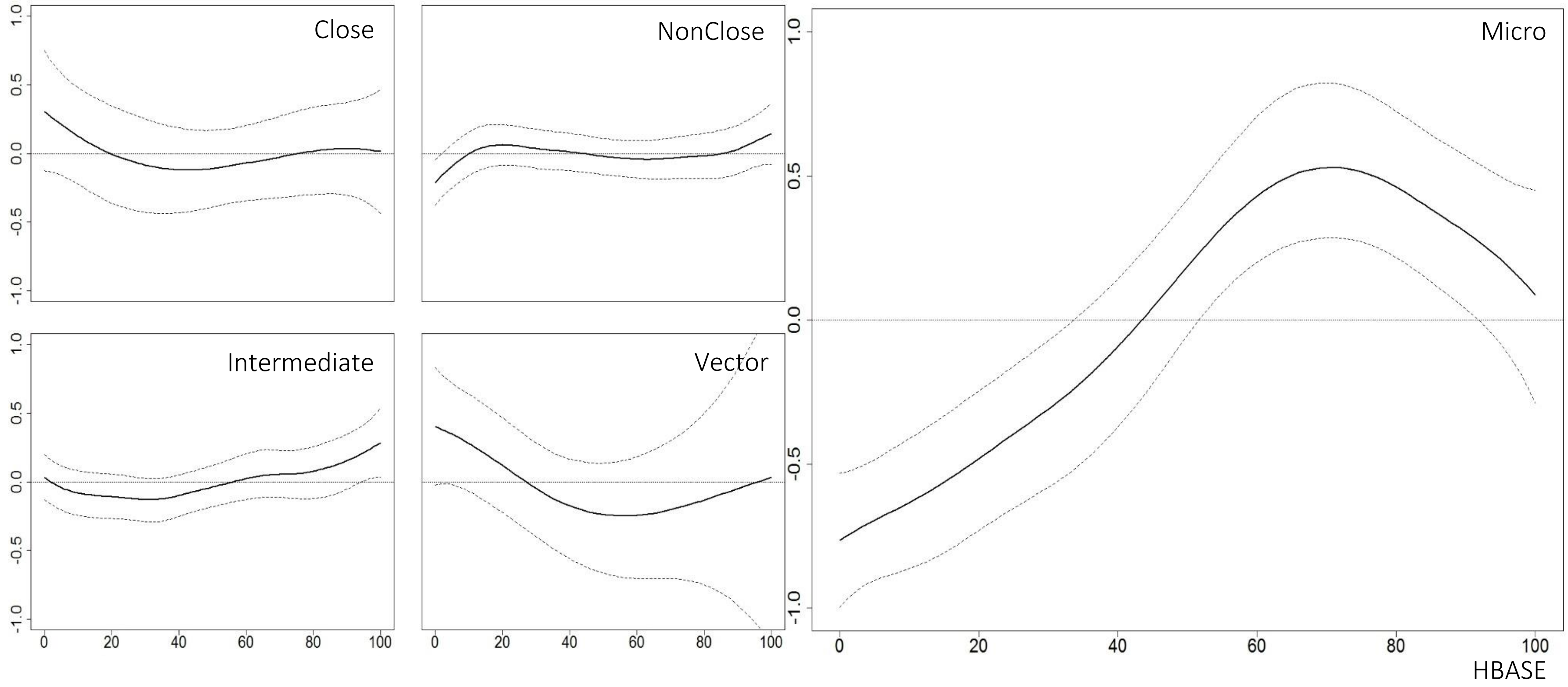

Figure 5.8 – Effect of HBASE (percentage of built-up space per area unit) the prevalence of infection categorised according to different parasite traits. HBASE scores are calculated on a 1x1Km area units derived from the GLS dataset. Dashed lines represent the 95% credible intervals, an effect is considered significant is the zero abline (dotted horizontal line) is not contained within the CI interval.

5.4.1.3 Spatial and temporal effect

The combined effect of the spatial and terms explained about 5% of the total variance of the model (Table 5.4). The temporal effect was modelled as a random walk of the first order; Figure 5.9 shows the effect of each year on the parasite probability of infection.

Figure 5.9 – Effect of each year on probability of infection of red foxes. The year effect is modelled using a random walk 1 model. The solid line shows the effect, while the dashed lines represent the 95% credible intervals.

The range corresponds to the distance at which the spatial correlation is close to 0.1, and it is positively correlated with a smoothness parameter λ and negatively correlated to a scaling parameter κ. The range is calculated according to the formula:

$$r = \frac{\sqrt{8\lambda}}{\kappa}$$

The spatial autocorrelation structure for this model had an estimated range of 3.9092degrees (credible intervals between 3.485 and 4.339), while the scaling parameter κ

was 0.726 (CI 0.648 - 0.805). Since each degree correspond to (approximately) 111Km, the range for this model was around 3433.9Km. Points closer together than 434Km, are considered to be spatially correlated (Figure 5.10).

Using the estimated parameters for range, scale and smoothness, along with the estimates for each variable included in the model, I can reconstruct the spatial representation of the underlying process characterising the response variable (in this case the probability of infection in foxes), which is then projected at each node of the mesh (Figure 5.11). This process follows a multivariate gaussian distribution and it is therefore called a Gaussian Random Field (GRF). Visually reproducing the GRF based on the model estimates is important as it show how the response variable changes in space, when all the variables included in the model are "stripped" away. This allows us to both visualise the

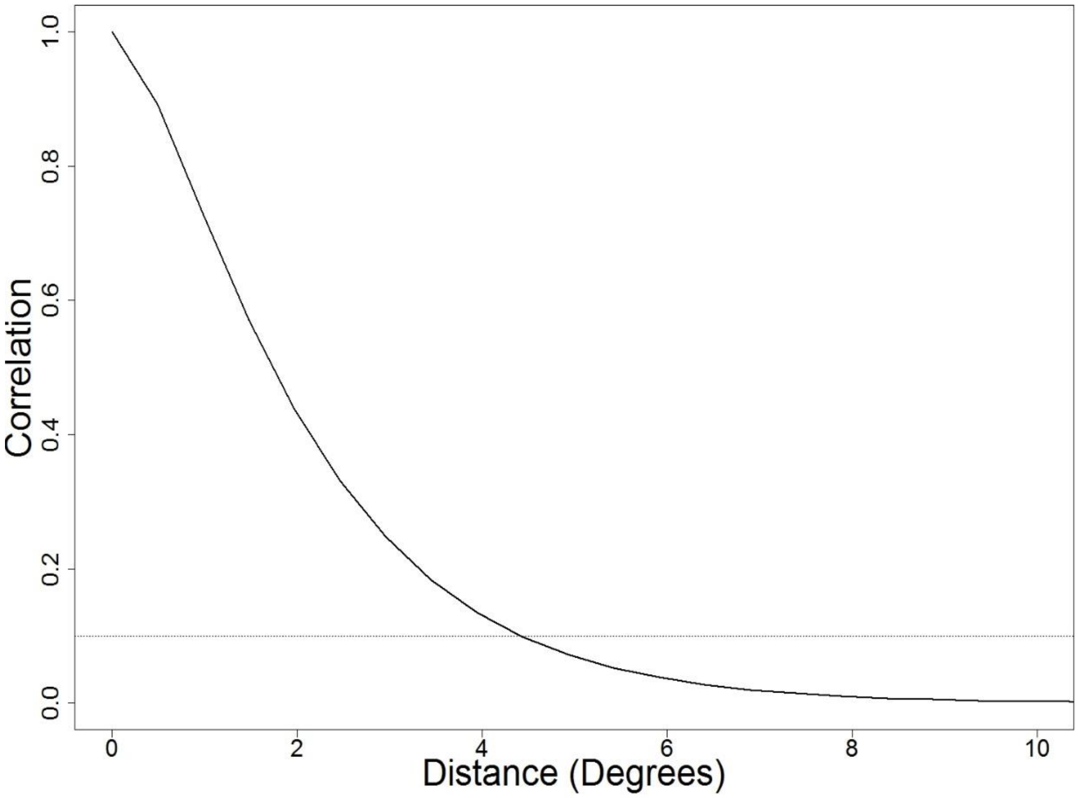

Figure 5.10 - Figure showing the spatial correlation structure over distance (in degrees) for model. The horizontal line shows the level of autocorrelation equal to 0.1, indicating that the range is approximately 3.909 degrees, or 433.9Km (intersection with the main line).

distribution of the variable of interest, as well as identify distinct spatial patterns, which can arise from missing variables.

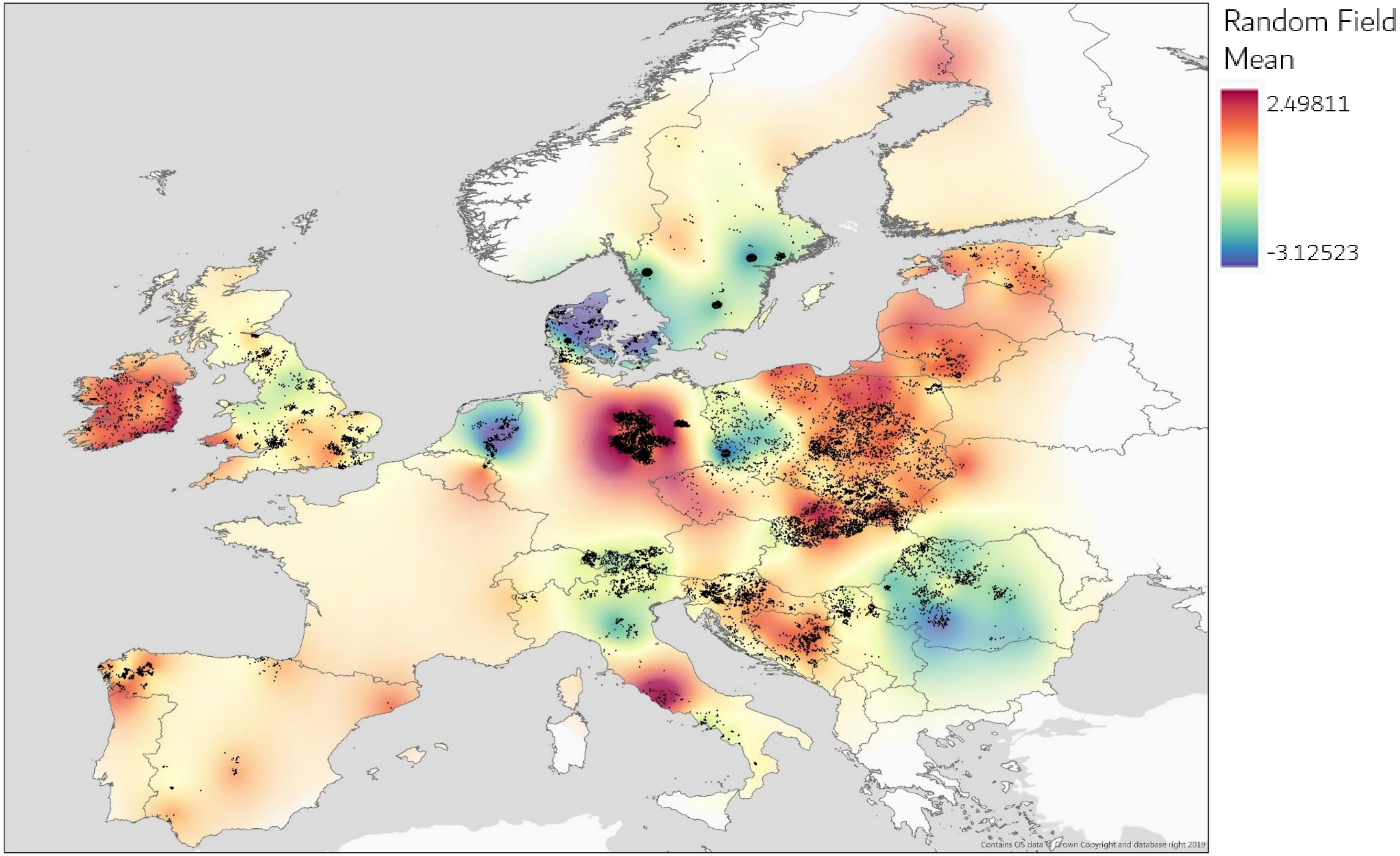

Figure 5.11 - Map showing the distribution of the spatial random field for the linear predictor in red to blue; red colour indicates a higher infection probability. Overlaid with the standard deviation layer, plotted in decreasing level of transparency (min = 0.249, max = 1.821). The autocorrelation range for this model was estimated to be approximately 430Km.

5.4.2 E. multilocularis Model

5.4.2.1 Linear Effects

Both latitude and temperature had a small but significant effect on the probability of infection of *E. multilocularis* in foxes (Table 5.5). Latitude was positively correlated with the response variables (foxes were more likely to be infected at locations that are more northern), while temperature was negatively correlated with it, with foxes being more likely to be infected at lower temperatures.

Effect	Mean	SD	Q 0.025	Q 0.975
Intercept	-6.1096	1.2338	-8.5448	-3.6961
Latitude	0.0807	0.0191	0.0434	0.1183
Temperature	-0.0927	0.0155	-0.1231	-0.0621

Table 5.5 – Linear effects included in the model fit to infer the probability of infection of E. multilocularis in red foxes. The linear predictors included latitude and temperature, the estimated effect, along with the standard deviation and credible intervals are also shown. An effect is considered significant if the CI do not include zero.

5.4.2.2 Non-Linear Effects

The combined spatial and temporal terms were the most important, accounting for almost 90% of the total variance in the model. Sample type and Detection method explained a comparable amount of variation (6.7% and 4.6% respectively), but Fox ID accounted for less than 0.1% of the total variation (Table 5.6); this is probably explained by the fact that foxes are not routinely tested multiple times, and there were only about 500 foxes that were tested using different methods. Finally, the effect of built-up percentage and footprint scores explained less than 0.1% of variance each.

Component	Variance explained	Proportion (%)
Range for spatial field	0.324	3.9
SD for spatial field	6.743	79.6
HBASE	1.31E-05	<0.1
FTPRN	6.77E-05	<0.1
Year	0.439	5.2
Fox ID	1.49E-05	<0.1
Sample Type	0.547	6.7
Detection Method	0.383	4.6

Table 5.6 – Table showing the variance explained by the non-linear effects included in the model, along with the relative proportion of each component.

Figure 5.12 shows the effect of built-up space percentage and footprint scores on the probability of foxes to be infected by *E. multilocularis*. HBASE effect did not seem to show any particular pattern and the effect is completely non-significant. On the other hand, the model showed a negative relation between the prevalence of *E.multilocularis* and the footprint score, with areas with a higher footprint score being associated with lower infection probability. However, the credible intervals were quite large, especially at low and high footprint values, and the effect is largely non-significant (only five levels over 51 have a significant effect).

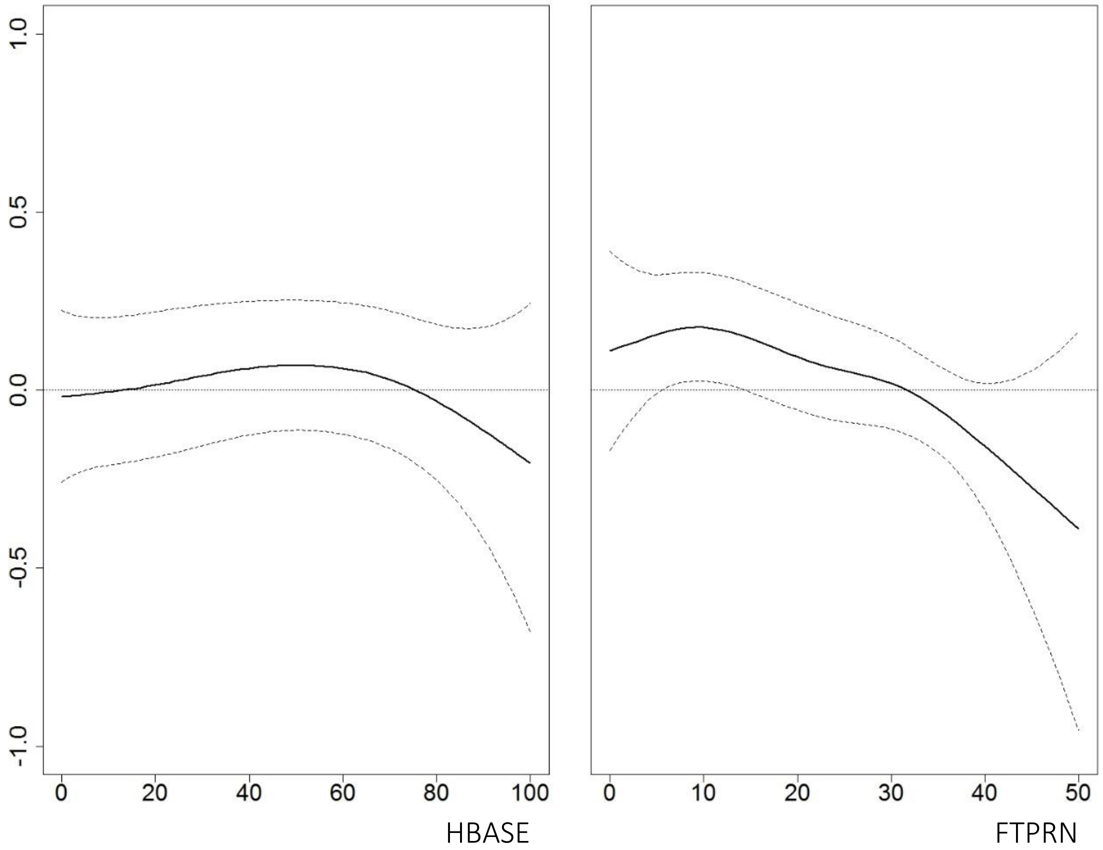

Figure 5.12 - Effect of built-up percentage (left) and footprint score (right) on the probability of infection of E. multilocularis in foxes. Dashed lines represent the 95% credible intervals, an effect is considered significant is the zero abline (dotted horizontal line) is not contained within the CI interval.

5.4.2.3 Spatial and Temporal Effect

The temporal effect showed a similar pattern to the one seen in the previous model (see Figure 5.9), with large variation even between consecutive years; in this case the effect was even more pronounced (Figure 5.13), probably due to the smaller sample size of this analysis. The model showed a range for the spatial autocorrelation of 3.217 degrees (CI 2.108 - 4.653), corresponding to ~ 357Km, while the scaling parameter was 0.917 (CI 0.567 - 1.258).

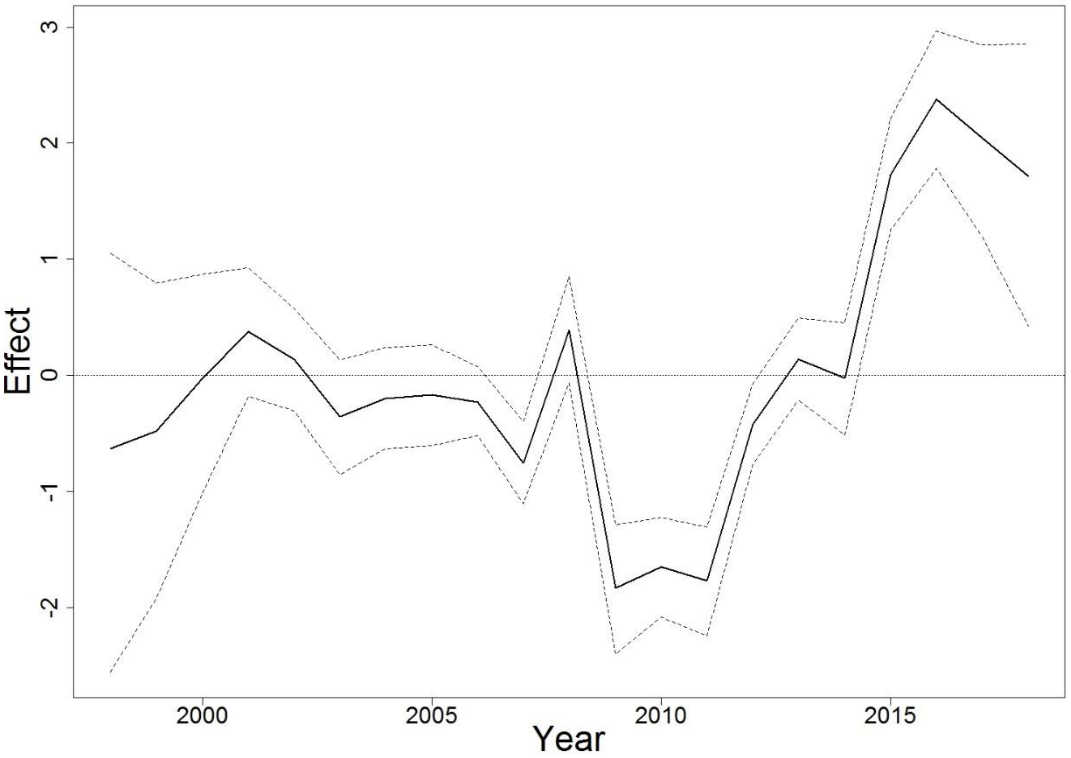

Figure 5.13 - Effect of each year on probability of E.multilocularis infection. The year effect is modelled using a random walk 1 model. The solid line shows the effect, while the dashed lines represent the 95% credible intervals.

The gaussian random field constructed using the model parameters can be found in Figure 5.14; it shows a distinct longitudinal pattern, with more eastern areas showing a higher probability of infection. Appendix 5c contains the non-layered projections of the mean and standard deviation for the random field for this model.

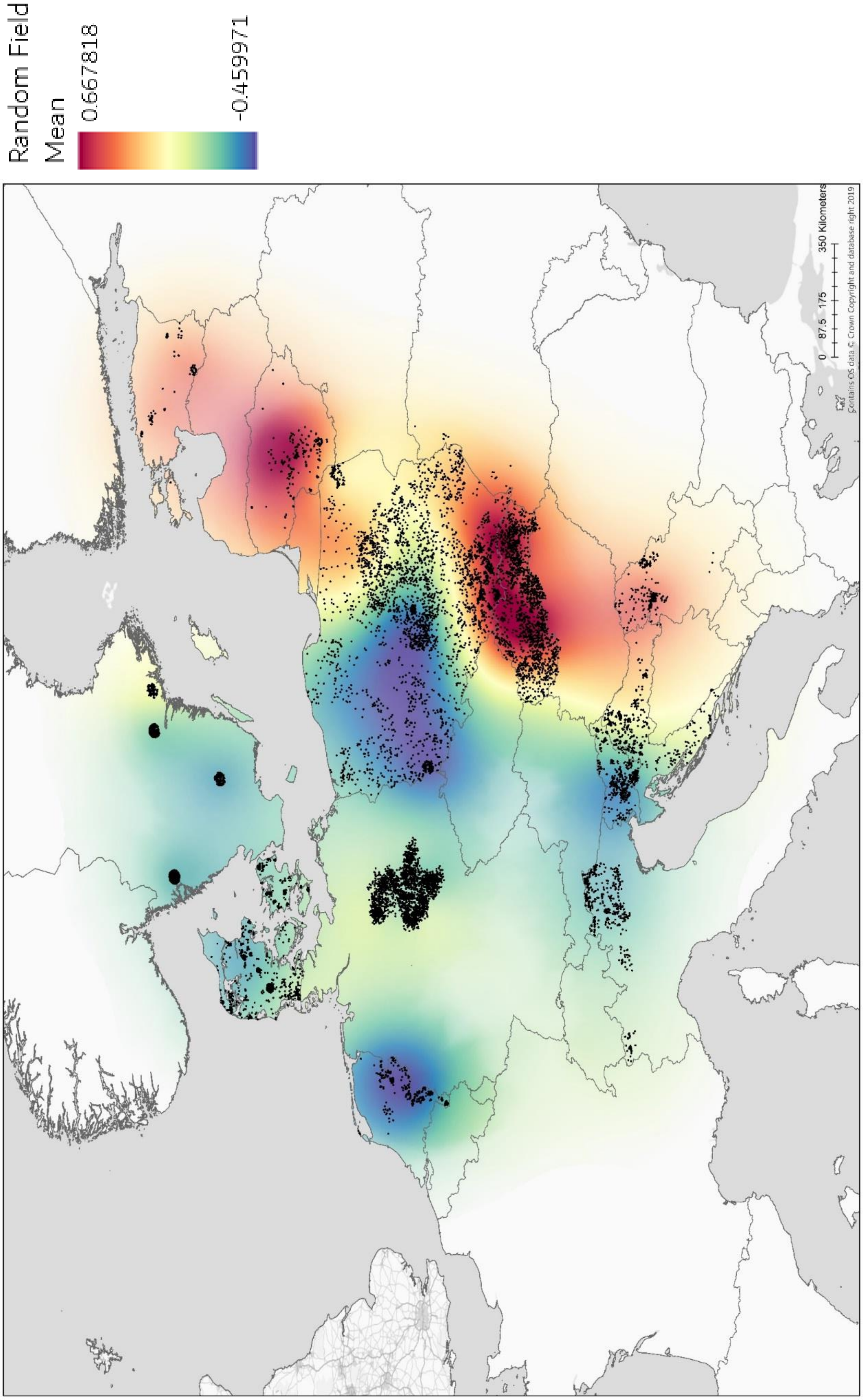

Figure 5.14 – Map showing the distribution of the spatial random field of the linear predictor for the E. multilocularis model (red to blue). Overlaid with the standard deviation layer, plotted in decreasing level of transparency (min = 0.131, max =0.306).

5.4.3 Future directions

Due to time and computational constrains, I was not able to present the models as they were originally intended. In particular, I plan to add two more features to the models:

- Construct a 3D mesh on the sphere

In this model, I used linear projections of latitude and longitude to model and plot coordinates, which is generally an acceptable approximation for small-scale studies. However, given the spatial extent of the dataset, I aim to construct a 3D mesh that would take into account the globe curvature and project the points on that mesh; this would give more accurate estimations of the spatial autocorrelation effect.

- Extend location uncertainty weights to the multi-parasite model

The weight term was only included in the smaller model (fitted on the *E.multilocularis* subset of the data); this was done for computational reasons, as including this increased the computational time of the model from 3 to 21 days. The weight term has been calculated for the entire dataset (the full weighted dataset includes around 1 million datapoints) and I intend to run the full model including a weight term, but this was unfeasible due to time constraints.

5.5 Discussion

5.5.1 Multi-parasite model

As expected, the heterogeneity in the response variable was responsible for most of the variation in the analysis (Table 5.4), with sample type, detection method and parasite genus together accounting for over 97% of the variance in the model.

Once I accounted for that variation however, a very clear trend emerged showing a distinct response of microparasites infection prevalence to increasing proportion of built-up space (Figure 5.8). This pattern follows remarkably closely the three zones identified by Guérois & Pumain (2008). The city centre maintains a very high (close to 100%) level of built-up space for 1-6Km around the centre, surrounded by an area of lower built-up level proportion (with a steep decrease to about 20-30%) and a gentler slope from there identifying peripheral areas leading to rural landscapes (Figure 5.15). The effect of HBASE ratio on microparasite

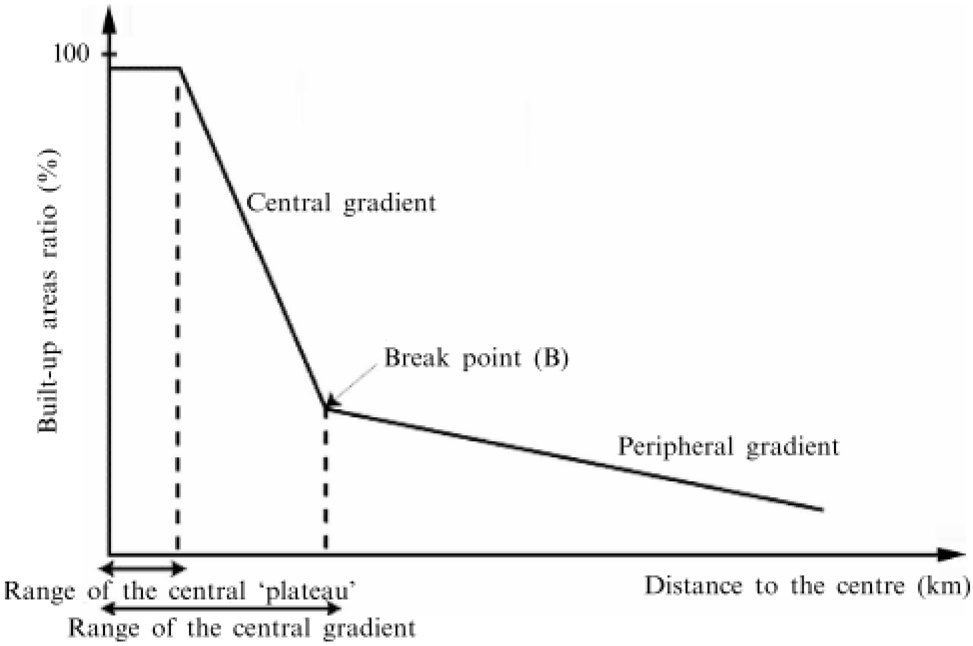

Figure 5.15 - pattern of decreasing levels of built-up space ratio at increasing distance from the city centre as presented by Guerois & Pumain. The ratio does not decrease linearly, but have two distinct breaks and different associated slopes. Source: Guerois & Pumain (2008).

infection is negative at low levels of built-up space (i.e. at low levels of urbanisation), but rise steadily and become positive between 40% and 50% of built-up space proportion. The effects keep increasing and peaks at moderately high levels of HBASE (between 70% and 80%), corresponding to the higher end of the suburban circle that surrounds the city centre, starting to then decrease again at higher HBASE scores (corresponding to the city centre). Microparasite infection dynamics rely on the availability of susceptible hosts, since individuals that have recovered from this kind of infection are generally immune (McCallum *et al.*, 2001). For this reason, both population density and population demographic structure can have a direct effect on the prevalence of this kind of infection.

The demography of urban foxes is dramatically different from that of rural ones; firstly, fox population density in urban areas is much higher than in rural landscapes (Gloor *et al.*, 2001). The effect of HBASE proportion on the prevalence of microparasites seems to follow closely the pattern of fox population density observed on the rural-urban gradient, where highly urbanised areas (such as city centres) are not suitable environments for foxes to live since they lack suitable denning sites for foxes to occupy (Harris & Trewhella, 1988). In contrast, medium level of urbanisation such as suburbs, which contain a higher proportion of greenspace such as gardens and parks, are a more suitable environment for foxes to live in (Harris & Rayner, 1986), resulting in higher fox densities. Furthermore, higher mortality rates (Doncaster & Macdonald, 1997; Baker *et al.*, 2007) and higher cub survival (Harris & Smith, 1987; Pagh *et al.*, 2018) both contribute to a greater proportion of young, naïve individuals in urban fox populations (Harris, 1977).

There is evidence to suggest the existence of a chain of factors determining the pattern of higher microparasite infection prevalence in areas that exhibit a moderate level of urbanisation; these areas proved particularly suitable to host populations of foxes characterised by high density and high mortality, resulting in a higher number of susceptible individuals, and ultimately resulting in the observed pattern.

However, I did not find evidence to support that directly transmitted pathogens were affected by the proportion of built-up space in the same way that microparasite infections were, even though I would expect this kind of infection be more prevalent at higher fox population densities (McCallum *et al.*, 2001). This is potentially due to the limitations of the dataset, since only about 2500 datapoints (3.4% of the dataset) were classified closely transmitted parasites, which suggests that the model might lack the power to detect the effect of HBASE on this kind of parasites.

Furthermore, it needs to be acknowledged that by the very nature of this dataset, the sampling effort is uneven throughout the study area, and this could be an important factor in determining the apparent distribution of parasite probability of infection, represented in the gaussian random field (GRF) presented in Figure 5.11. While I accounted for detection method in my analyses, it is near impossible to exactly quantify the level of accuracy of each detection method, which could be a source of bias in the representation of the geographical distribution of parasite infection. For this reason, while I believe that the effect of built-up space ratio on the probability of infection of microparasites is real and accurately represented in my models, the representation of the GRF should not be taken as an accurate map of fox infection prevalence over Europe, and its main purpose should be to identify areas where more data should be sourced in order to achieve a more realistic representation of the real distribution of fox infection dynamics.

5.5.2 Echinococcus multilocularis model

The second model was fit to determine the effect of human footprint (FTPRN) and built-up space proportion (HBASE) specifically on the *Echinococcus multilocularis* probability of infection.

Like in the multi-species model, the amount of variance explained by the effects of both the FTPRN and HBASE terms were small (<0.1%), suggesting a limited impact of urbanisation on the disease ecology of this parasite. On the other hand, the spatial term explained a high proportion of the variance (over 80%). This is reflected in the projected random field for the model (Figure 5.14) that shows a clear longitudinal gradient, with increasing *E. multilocularis* prevalence from east to west. Since the data are based on surveys carried out in areas where *E.multilocularis* is considered endemic (European Centre for Disease Prevention and Control, 2018), it is surprising to see such a clear spatial pattern in the infection prevalence. This could indicate an expansion in the distribution of this parasite towards Eastern Europe. Noticeably, the random field of the model accurately predicted a high prevalence of *E. multilocularis* at the border between Poland and the Slovak Republic (see Davidson *et al.*, 2012) and a shift from low prevalence to high prevalence between western and eastern Poland (See Oksanen *et al.*, 2016). However these results should be taken carefully since the dataset is not comprehensive and it does not achieve a comprehensive data coverage in some areas that are considered to be highly endemic regions, such as Eastern France, Switzerland and South-West Germany (Oksanen *et al.*, 2016).

The effect of urbanisation on the prevalence of *E. multilocularis* in foxes has been extensively investigated, particularly in countries where this parasite is considered to be highly endemic (e.g. Germany, France and Switzerland). In particular several studies from Switzerland (e.g. Hofer *et al.*, 2000; Stieger *et al.*, 2002; Hegglin *et al.*, 2007; Reperant *et al.*, 2009), have found a lower prevalence of this parasite in foxes from urbanised areas. In a consequent review, they hypothesis that this was the result of a decreased predation rate on the intermediate host (mainly Arvicolidae), driven by the high availability of alternative anthropogenic sources of food for foxes (Deplazes *et al.*, 2004). I specifically tested this hypothesis by including the transmission traits in the multispecies model, but did not find any evidence to suggest that urbanisation level has any impact on the prevalence of parasites that require an intermediate host (Figure 5.8).

On the other hand the results of the model fit on the *E. multilocularis* subset of the data, show at least some evidence to support the theory that increased levels of anthropogenic pressure can decrease the prevalence of this parasite (Figure 5.12). However, rather than the proportion of built-up space (which is a more explicit measurement of urbanisation), it was the measure of urban footprint that showed a negative correlation to the prevalence of *E.multilocularis*.

Human footprint is a composite measure of the direct and indirect human pressures on the environment (Venter *et al.*, 2016); it includes measurements relating directly to urbanity, such as human population density and road cover, but also extent of crop and pasture land and the presence of railways and navigable waterways. It is a more inclusive measurement of the level of modification of the environment, rather than focusing solely on the level of urbanity. However, the very nature of this measurement makes it hard to draw clear conclusions and to reach a proper understanding of the mechanism behind this effect. Furthermore, the credible intervals calculated for the footprint effect were very wide, especially at very low and very high levels of human footprint, making harder to draw definitive conclusions; repeating this analysis including more data could help understand the true effect of this term.

The effect of urbanity is a complex one and, while it is important to analyse large dataset in order to identify underlying patterns, trying to bring together data from vastly different studies is challenging. The models I presented in this chapter represent my effort to synthesise the available data and are hopefully a first step towards disentangling this complex and multifaceted problem.

5.6 Acknowledgements

This work could not have been possible without the collaboration of the research groups who collected and published the data, and agreed to share them with me. For this reason, I wish to thank Andrea Balboni, Eva Bartova, Reljia Beck, Łukasz Binkoswki, Claudio De Liberato, John Debenham, Nicolai Denzin, Rita Di Cerbo, Alfredo Fiocchi, Hans-Peter Fuhrer, Jakub Gawor, Pierre Gras, Adnan Hodzic, Heidi Huus-Petersen, David Anton Jimenez, Jacek Karamon, Age Karssin, Vitaliy Kharchenko, Dusan Lalosevich, Vesna Lalosevich, Andrei Mihalca, Gianluca D'amico, Georgiana Deak, Mirabela Dumitrache, Patrick Foley, Javier Millán, Andrea Miller, Guadalupe Miró, Martina Miterpakova, Eric Morgan, Emma O'Neil, Urmas Saarma, Mario Santoro, Mindaugas, Šarkūnas, Alen Slavica, Peter Stuart, Gorazd Vengušt.

This list is not comprehensive, as it only includes the names of the people with whom I have been corresponding. Many other have contributed to the data collection, including field assistants, lab technicians and other collaborator; it would be impractical to list them all here, but I am deeply grateful to everyone who has contributed to this project. I would also like to personally thank Dr Dishon Muloi for his invaluable help in the classification of parasite traits, and Prof Finn Lindgren for invaluable advice on how to best adjust the model.

Chapter 6

General Discussion

“A Flatterers thrive on fools' credulity.
The lesson's worth a cheese, don't you agree?"
The crow, shamefaced and flustered swore,
Too late, however: "Nevermore!"

The Fox to the Crow
Moral of the fable “Le Corbeau et le Renard”
La Fontaine (1841)

6.1 Thesis scope

In an increasingly urbanised world, urban areas should not be overlooked by ecological research (Goddard et al., 2010). The emergence of zoonotic pathogens (Wilcox & Gubler, 2005) and the transmission of zoonotic parasites at the human-wildlife interface, makes disease ecology research in urban area a particularly important field of research (Bradley & Altizer, 2006). In the context of European urban areas in particular, Red foxes (Vulpes vulpes) are one of the most successful mammalian species in colonising urban areas (Teagle, 1967; Gloor et al., 2001; Guislain et al., 2008; Kauhala et al., 2015), and one of the main focus of epidemiological studies. Some of the Zoonoses carried by foxes, such as rabies (Anderson et al., 1981) and most recently the tapeworm Echinococcus multilocularis (Raoul et al., 2015), are among the most serious pathologies that can infect humans at temperate climates (Kruse et al., 2004) and it is not surprising that a vast body of research has been carried out on the subject. However, the complex nature of urban landscapes and the difficulty in finding an objective and comprehensive definition of what constitute an urban area (Sayer, 1984), has hindered efforts to generalise research finding beyond the local context. The aim of this thesis was to investigate the ways in which urban environment can affect host-parasite dynamics of urban red foxes; I used different approaches to identify both small- and large-scale patterns, as presented in chapter 2 through 5.

6.2 Key findings

6.2.1 Chapter 2.

Chapter 2 can be considered a prologue to the entire thesis; there, I conducted a pilot study to evaluate the use of stable isotopes analysis (SIA) to detect the amount of anthropogenic food in the diet of a fox, using hair samples from urban and rural areas from the UK. The availability of virtually unlimited anthropogenic food in urban areas is one of the main characteristics contributing to the uniqueness of this environment and one of the major factors in shaping urban ecological communities in general and host-parasite dynamics in particular (Becker *et al.*, 2015). However, classic diet analysis techniques are inadequate to detect and measure the amount of anthropogenic food in the diet of wild carnivores (Fascione *et al*., 2004); promising results have been shown in using SIA for this purpose in North America, where the presence of corn syrup in most of human-produced food causes a shift in the Carbon isotope fingerprint of this kind of food (Newsome *et al.*, 2015). However, the results of this pilot studies showed no differences in the isotopic niche of urban and rural foxes from the UK, indicating that either the isotopic footprint of anthropogenic food in the UK is not different from the one of natural food sources, or that urban and rural foxes from the UK do not have a significantly different diet, and hence the difference is not measureable. In any case, the results of this analysis show that for the purpose of this thesis, direct measurements of anthropogenic food consumption in urban foxes were not available and hence were not included explicitly any other analysis.

6.2.2 Chapter 3 and Chapter 4.

Chapters 3 and 4 should be considered together as two aspects of the same investigation; in these chapters, I investigated the ways spatial and temporal changes in the urban landscape can influence the gastrointestinal (GI) parasite community of urban foxes.

In chapter 3, I attempt to describe the urban landscape by using several socio-economic and ecological variables; these were measured separately across the urban landscape, to determine which ones are important in determining fox territorial marking patterns and GI parasite prevalence and diversity. By using an objective, multivariate definition of urbanity, I purposely avoided a binary classification of what constitutes an urban site. I found that the proportion of greenspace around a site was the single stronger predictor for all the response variables; greenspace ratio was positively associated with the number of fox scats found in a site, parasite diversity, species richness and likelihood of infection. This indicates that landscape fragmentation is one of the main factors affecting fox ecology, potentially by altering their territoriality and movement behaviour (Gras *et al.*, 2018); sites that are better connected tend to be marked heavily. In turn the higher density of scats in heavily marked sites can increase the infective pressure of GI parasite on foxes, resulting in a higher prevalence and diversity of parasites. Landscape fragmentation and greenspace are metrics rarely taken into account in urban disease ecology studies, but my results show that this metric should be routinely included in this kind of studies.

In chapter 4 I used similar methods for scat collection and parasite identification, but I applied them to a much smaller set of sites, which I surveyed intensively for nine months, in order to collect longitudinal data relative to temporal patterns of parasite prevalence, burden and diversity.

I used a multi-model approach (Brook & Bradshaw, 2006) to determine the best temporal structure for each response variable. I found that a site-specific structured temporal effect was the best fit for almost all models, suggesting that small scale variation in the urban area can influence the parasite dynamics of the individual sites. In addition, I also found a limited effect of microclimatic conditions (temperature and humidity) and a much stronger positive relationship between the presence of some prey items (such as rabbit and micromammals) and parasite diversity. This is in line with the more stable climatic conditions found in urban areas ("the pseudo-tropical bubble" as defined by Shochat *et al.*, 2006), that can hamper seasonal dynamic of soil-borne parasites. The effect of the prey items on parasite diversity can be interpreted as an indication that a more natural diet is correlated with a higher parasite diversity, but since I lacked reliable data on anthropogenic food consumption, I cannot draw definitive conclusions.

Together these results show the effect that the heterogeneity of the urban landscape have on spatio-temporal patterns of GI parasites dynamics; the heterogeneity of urban landscapes can lead to complex patterns in the distribution and dynamics of parasites prevalence, burden and diversity. Incorporating measureable elements of the urban environment can significantly improve our understanding of the processes driving host-parasite dynamics, both spatially and temporally.

6.2.3 Chapter 5

Understanding the specific drivers of host-parasite dynamics at a local scale can be useful to design specific management plans (Farrell *et al.*, 2013), and are very important for the monitoring and control of zoonotic diseases at country- or regional level (Westrell *et al.*, 2009). However, the heterogeneous nature of urban areas makes it difficult to draw general conclusions, despite the vast body of parasitological research conducted on fox in Europe.

In chapter 5 I aimed to develop a model that would allow to draw a synthesis of the available data, in order to determine the overall effect of urbanisation on the prevalence of fox parasites. I collated a georeferenced dataset using raw data from previously published studies and accounted for heterogeneity in the focus species by categorising each parasite taxon on the basis of transmission traits and parasite type (micro- vs macroparasite). I then used a spatio-temporal model to fit parasite presence as a function of urbanity level, using high-resolution (1Kmx1Km) remote sensing data of built-up space as a measurement for urbanity. The results of this model show a clear response of microparasites to urbanity level, with a pattern that peaks at medium (~70%) levels of built-up space. This suggests that fox density (which is highest in suburbs and medium-density housing areas ;Harris & Rayner,

1986) is a major factor in determining the probability of micro-parasite infection and the high fox population densities measured in urban areas could result in higher risk of zoonotic emergence (Hassell *et al.*, 2017). The variance explained by study-specific attributes (parasite taxon, detection method and sample type), was by far the highest (over 95%), confirming that the model successfully accounted for the heterogeneity in the dataset generated by variation in the method of investigation.

I also fitted a similar model on a subset of data referring on a single parasite species: the *Echinococcus multilocularis*. A common theory regarding the effect of urbanisation on this parasite is that the amount of anthropogenic food in urban areas lower the level of predation on intermediate hosts (mainly voles) by foxes, disrupting the parasite cycle and ultimately resulting in a lower prevalence of *E. multilocularis* in more urbanised areas compared to more natural landscapes (Deplazes *et al.*, 2004; Liccioli *et al.*, 2015); furthermore, *E. multilocularis* represented the most common parasite in my dataset, with more than 12000 datapoints referring to this taxon. I applied a modified version of my spatio-temporal model to the *E. multilocularis* data in order to determine if there was a measureable effect of urbanity, and found some evidences that human footprint (but not built-up space) could have a negative impact on the probability of a fox to be infected by *E. multilocularis*. However, the credible intervals were relatively large, hence these results should be taken carefully

The results from this chapter paint a broad picture of the overall effect of urbanity on the disease ecology of red foxes; this effect is complex and not universal among different parasite species, but follow broad pattern of interaction with certain parasite traits. More importantly, this kind of models proved a valid alternative to classic meta-analysis of highly heterogeneous data, and especially relevant in the field of urban ecology, where it is difficult to bring together data from studies using subjective (and hence non-comparable) definitions of urbanity.

6.3 Final remarks

The main objective of my project was to determine the effect that urbanisation can have on the disease ecology of urban foxes. This is simply not possible while relying on subjective classification based on the urban/rural dichotomy.

In this thesis, I explored the multiple variables that can affect the parasite community of foxes in a single urban area, and I attempted to define the overall effect of urbanity on parasite prevalence by drawing a synthesis of available data. While these two approaches might seem antithetical at a first glance, they are in fact the two sides of the same coin. Given the variation in the individual characteristics of the urban landscapes, it will never be possible to explore specific dynamics that occur in each individual city using a large-scale model; at the same time, being able to synthesise local data and understand general dynamics common to every urban environment, is a powerful tool and should not be dismissed.

I hope I showed that it is possible to move beyond the “low-hanging fruit” of urban/rural dichotomy (Mcdonnell & Hahs, 2013), and define urbanity as a function of objective and measureable variables. Urban/rural comparison can still be useful in the context of a single city, but the distinction should be done on the basis of more rigorous (and preferably multivariate) criteria, so that the results can be replicated and compared with other studies. As efforts to produce global datasets of urban-defining metrics increase (i.e. nightlights, Zhang & Seto, 2011; built-up space, Wang *et al.*, 2017; or composite metrics Venter *et al.*, 2016; Alsaaideh *et al.*, 2017 to cite just few), more resources are becoming widely available in modelling the effect of urban environment on parasite communities of city dwellers.

Ultimately, it might never be possible to produce a comprehensive, objective and universally valid definition of urbanity, as the differences between “urbes” are too vast. However, accounting for element of spatial variation in the urban fabric represents a first step in the direction of a more comprehensive understanding of the ways in which urban environment affects ecological communities.

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Appendices

Appendix 3a

I was unable to identify one of the parasites I found during the investigations reported in chapters 3 and 4 beyond genus level (*Strongyle spp*) or even to confirm that it was a fox parasite; it was suggested it might have been present in the foxes digestive trait following ingestion of infected prey items (pers.comm., E. Morgan); this explanation seemed to be confirmed by independent researcher who recognised this parasite (although they could not taxonomically identify it) as they found it in the digestive trait of rabbit (pers.comm. B. Boag) and wood mice (pers.comm A. Sweeny) from Scotland. However, both in mice and rabbit, this parasite was very rare (both researchers reported a very low prevalence of these parasites in their study system), while in this study it represented the third most common helminth, with a prevalence of over 30%, suggesting that foxes could be a competent host.

I report here a series of pictures taken during the flotation analysis (FIG), alongside with the measurements of each of the axes (A3.2). In total I took pictures of 344 specimens, the average length of the short axis was 30.351µm (sd = 2.615), and the average length of the long axis was 59.291µm (sd = 8.312).

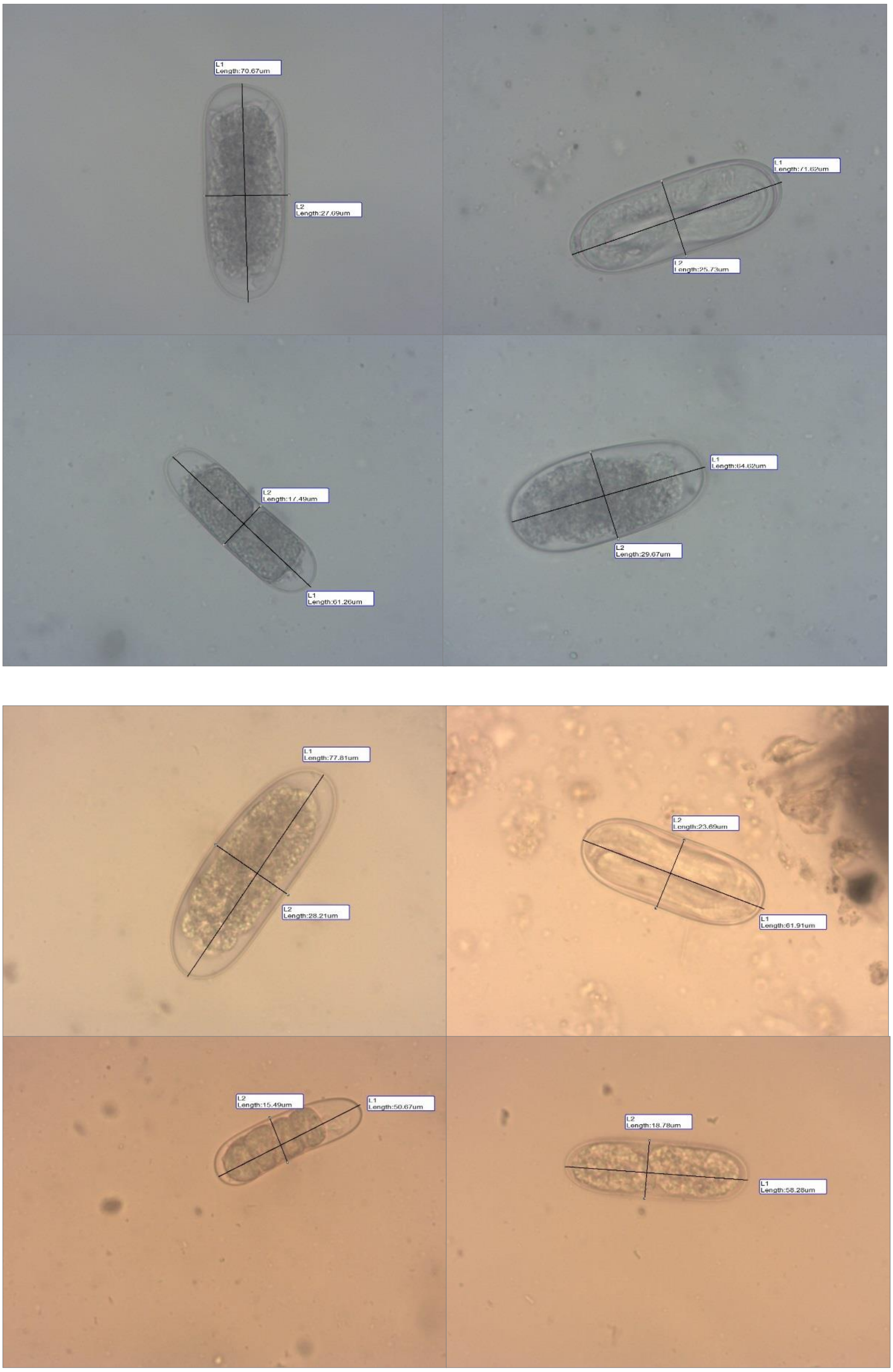

Figure A3.1 – pictures taken during the flotation analysis performed on the faecal samples collected around Edinburgh (full report of the results can be found in CH3). The different colouration of the pictures depends only on the microscope settings.

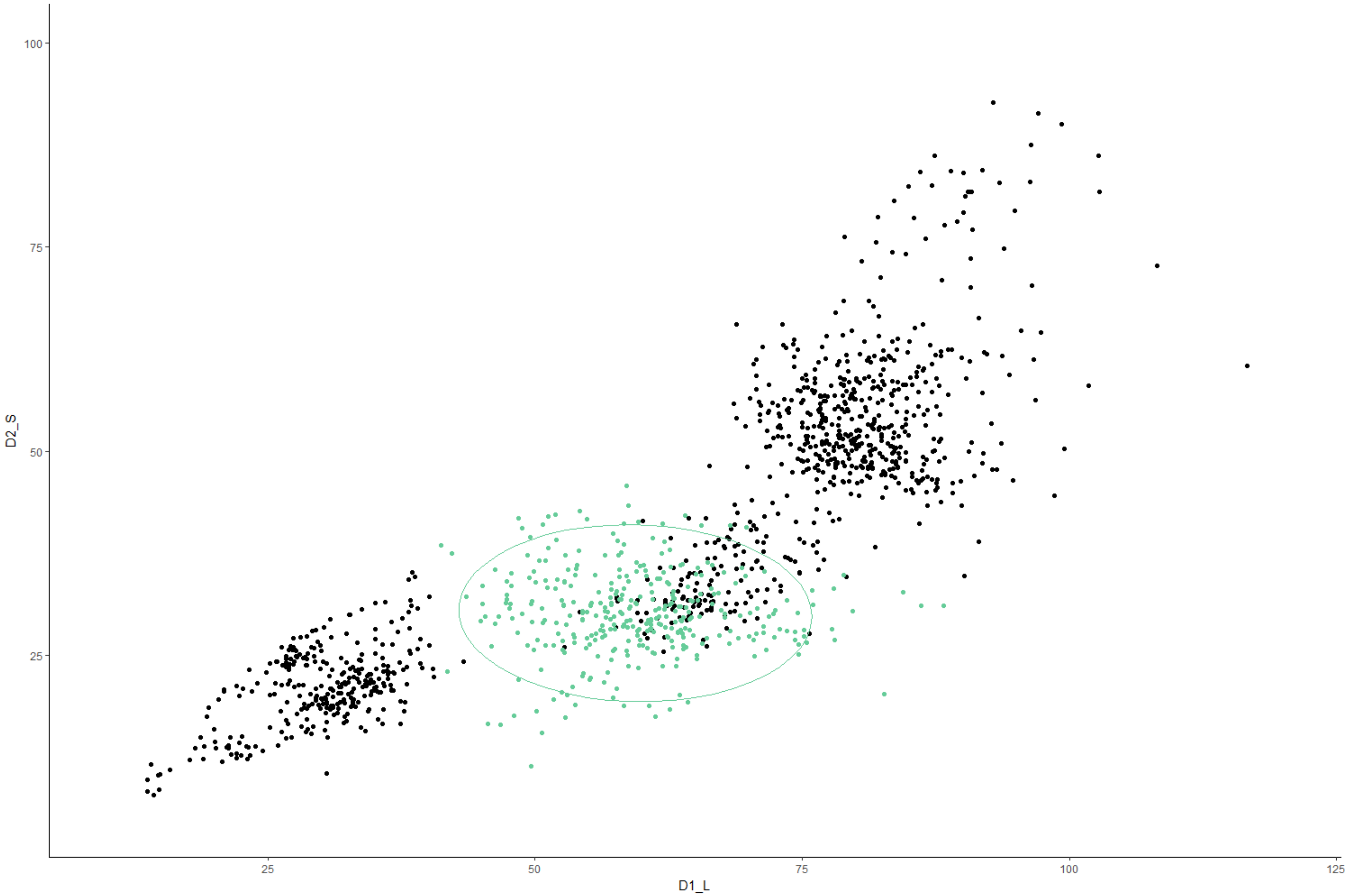

Figure A3.2 - figure showing the measurements for the two axes measurements of each parasite egg/oocyst found during the investigation. The long axis is displayed horizontally (plot x axis), while the short axis is displayed vertically (plot y axis). The points referring to the unknown strongyle are highlighted in green (the ellipse encompasses 95% of the data).

Appendix 3b

Here, I report the model output for the species-specific models were run to evaluate the effect of socio-economic and ecological variables on the infection risk (presence/absence; Table A3.1) of each parasite taxa identified form red fox faecal samples collected across green spaces sites throughout the urban landscape of Edinburgh UK. The models fit to *Taenia spp* nor the *T. canis* burden model did not data converge and are hence omitted

	Euculeus Aerophilus			*Uncinaria stenocephala*			*Toxocara canis*			Coccidia		
Fixed effects	Estimate	SE	t-value	Estimate	SE	t-value	Estimate	SE	t-value	Estimate	SE	t-value
Intercept	4.821	3.264	1.477	-1.177	1.211	-0.971	-24.356	8139.40	-0.003	1.384	3.452	0.401
Road Cover	0.106	0.213	0.497	0.195	0.239	0.816	0.523	0.476	1.100	0.249	0.221	1.124
Traffic counts	0.236	0.171	1.373	0.249	0.183	1.363	0.403	0.281	1.434	-0.079	0.205	-0.384
Population Density	0.284	0.180	1.577	-0.127	0.195	-0.652	-0.294	0.354	-0.830	0.072	0.215	0.335
Green Space Ratio	2.347	1.475	1.591	**3.442**	**1.689**	**2.037**	4.536	3.417	1.327	0.422	0.260	1.622
Green Space Variability	0.358	0.207	1.728	0.233	0.226	1.029	0.592	0.420	1.408	-0.076	0.216	-0.355
Sampling period (Autumn)	**-1.069**	**0.334**	**-3.199**	0.083	0.334	0.250	0.134	0.530	0.253	0.083	0.261	0.317
Site Area (Log)	-0.939	0.679	-1.382	-0.843	0.739	-1.141	18.618	8139.39	0.002	0.998	0.7107	1.405
Urban Wilderness (1)	**-1.616**	**0.740**	**-2.182**	0.271	0.786	0.345	19.431	8139.39	0.002	**1.835**	**0.799**	**2.296**
Urban Wilderness (2-3)	-0.554	0.411	-1.345	-0.169	0.240	-0.708	0.115	0.783	0.148	-0.358	0.433	-0.826
Managed Vegetation level (1-2)	-0.074	0.654	-0.113	-1.174	0.749	-1.567	-1.055	1.466	-0.720	0.0503	0.693	0.073
Managed Vegetation level (3-4)	-1.058	0.586	-1.805	-1.095	0.637	-1.717	-0.864	1.165	-0.742	-0.373	0.595	-0.628
Random effects	Variance			Variance			Variance			Variance		
Site ID	5.22 e^{-09}			5.15 e^{-09}			0.6614			0.5458		
Spatial effect	0.0556			0.2507			6.64 e^{-10}			0.0556		

Table A3.1 *The GLMM model output for the single-species parasite prevalence (presence/absence) regarding E. aerophilus, U. stenocephala, T. canis and coccidian parasites. 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. Significant terms are highlighted in bold (t-values higher than 2 are considered significant). The results regarding the Taenia spp data are not included since the model did not converge.*

Appendix 4

Here I report average temperature, humidity and dew point values calculated for each survey week in 2018 (Table A4.1). The measurements were taken using data loggers taking measurements once per hour for the duration of the study (13 weeks). The values reported for the BY site were downloaded from the GSOD dataset since it was not possible to retrieve the data logger in that site at the end of the survey.

Survey Week	Site	Temp C°	Dew Point C°	Humidity %
FW01	BH	1.302	0.758	88.056
FW01	CL	NA	NA	NA
FW01	DL	1.823	2.195	78.070
FW01	HD	0.352	0.994	88.204
FW01	LH	2.654	5.117	67.380
FW02	BH	1.967	1.989	102.987
FW02	CL	1.809	2.419	94.053
FW02	DL	2.355	1.901	97.823
FW02	HD	1.654	2.107	97.337
FW02	LH	1.607	1.796	103.721
FW03	BH	3.427	1.896	102.504
FW03	CL	3.823	2.875	92.132
FW03	DL	5.008	4.840	91.255
FW03	HD	3.386	2.282	96.281
FW03	LH	3.144	2.028	107.312
FW04	BH	7.438	2.039	101.098
FW04	CL	9.184	4.687	85.114
FW04	DL	10.293	5.841	89.021
FW04	HD	7.957	2.694	94.053
FW04	LH	7.664	2.456	105.662
FW05	BH	9.253	2.928	90.317
FW05	CL	11.407	5.579	73.872
FW05	DL	11.036	3.423	93.557
FW05	HD	9.524	3.072	87.377
FW05	LH	9.672	3.255	102.851
FW06	BH	11.640	2.204	94.728
FW06	CL	12.865	3.682	86.129
FW06	DL	12.205	1.668	97.344
FW06	HD	11.462	2.241	93.921
FW06	LH	12.223	2.489	101.556

FW07	BH	12.322	2.532	92.624
FW07	CL	13.159	3.799	82.624
FW07	DL	12.936	2.1476	99.087
FW07	HD	12.633	3.018	86.593
FW07	LH	13.062	3.053	101.389
FW08	BH	15.181	2.482	85.323
FW08	CL	16.247	3.362	77.365
FW08	DL	15.502	2.231	92.172
FW08	HD	15.717	2.835	80.712
FW08	LH	15.755	2.939	93.893
FW09	BH	14.531	2.592	96.257
FW09	CL	15.620	3.544	83.714
FW09	DL	15.471	2.227	98.484
FW09	HD	15.231	3.211	86.409
FW09	LH	15.295	2.670	103.067
FW10	BH	12.591	1.872	102.354
FW10	CL	13.092	2.350	90.309
FW10	DL	13.753	1.439	102.271
FW10	HD	12.875	2.259	94.326
FW10	LH	13.441	1.811	106.036
FW11	BH	10.367	2.344	97.721
FW11	CL	10.619	2.844	87.420
FW11	DL	11.479	1.964	98.010
FW11	HD	10.486	2.781	90.276
FW11	LH	10.632	2.244	105.830
FW12	BH	9.627	2.611	98.307
FW12	CL	10.008	3.151	86.979
FW12	DL	10.457	2.151	97.730
FW12	HD	9.815	3.105	90.802
FW12	LH	9.470	2.512	104.159
FW13	BH	7.212	2.243	101.887
FW13	CL	6.700	2.918	90.687
FW13	DL	7.445	1.856	102.958
FW13	HD	6.699	2.797	96.441

Appendix 5a

List of papers satisfying the inclusion criteria for the spatial analysis. Emails were sent to the corresponding author for each of these papers.

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Appendix 5b

List of acronyms used for the non-linear (random) effect included in the spatial models to control for sample type and detection method. Parasite location was also recorded (defined as site of main infection), but it was not included in the final model (Table A5.1).

I also report the table with the classification of each parasite taxon according to parasite genus, parasite family, the four transmission traits (Close-, NonClose-, Intermediate-, and Vector), the type of infection cause (acute/chronic), the parasite type (micro- or macro-), and parasite location (Table A5.2).

Sample type		Method		Parasite location	
ANI	Whole animal (alive)	ClinEx	Clinical examination	LUN	Lungs
BLOOD	Blood sample	ELISA	ELISA analysis	BL	Blood
CAR	Whole carcass	FEC	Faecal egg count	HEA	Heart
FAEC	Faecal sample	HIST	Histological examination	BLAD	Bladder
HEART	Heart	IFAT	Indirect Fluorescent Antibody Technique	BR	Brain
LIV/KID	Liver and Kidneys	IMF	Immunofluorescence	LIV	Liver
LUNGS	Lungs	MYF	Merthoilate-Yodine-Formaline sedimentation	SKN	Skin
MUS	Muscle sample	NEC	Necroscopy	ST	Stomach
SER	Serum sample	PCR	PCR	INT	Intestine
SPLEEN	Spleen	SCT	Sedimentation and counting Technique		
		SER	Serology		
		SWAB	Swab		

Table A5.1 – List of the acronyms used in chapter 5: the type of sample analysed, the type of analysis used to detect parasite presence/absence and location of the main parasite infection (parasite-specific)

Table A5.2 - classification of all parasite taxa included in the meta-analysis (Chapter 5). This includes the transmission traits (Close, NonClose, Intermediate, Vector), the disease type (Acute/Chronic) and the parasite type (Micro/Macro)

Parasite Spp	Parasite Genus	Parasite Family	Close	NonClose	Vector	Int_Num	Int_spp	Acute	Chronic	Parasite Type	Location
		Coccidia	0	1	0	0	0	0	1	Micro	INT
Cryptosporidium.canis	Cryptosporidium	Cryptosporidiidae	0	1	0	0	0	0	1	Micro	INT
Cryptosporidium.felis	Cryptosporidium	Cryptosporidiidae	0	1	0	0	0	0	1	Micro	INT
Cryptosporidium.parvum	Cryptosporidium	Cryptosporidiidae	0	1	0	0	0	0	1	Micro	INT
Cryptosporidium.ubiquitum	Cryptosporidium	Cryptosporidiidae	0	1	0	0	0	0	1	Micro	INT
Cystoisospora.canis	Cystoisospora	Eimeriidae	0	1	0	0	0	0	1	Micro	INT
	Eimeria	Eimeriidae	0	1	0	0	0	0	1	Micro	INT
Isospora.melis	Isospora	Eimeriidae	0	1	0	0	0	0	1	Micro	INT
	Isospora	Eimeriidae	0	1	0	0	0	0	1	Micro	INT
Hepatozoon.canis	Hepatozoon	Hepatozoidae	0	0	ticks	0	0	1	0	Micro	BL
Neospora.caninum	Neospora	Sarcocystiidae	0	0	0	1	mammals	0	1	Micro	BR
	Sarcocystis	Sarcocystiidae	0	0	0	1	mammals	0	1	Micro	INT
Toxoplasma.gondii	Toxoplasma	Sarcocystiidae	0	0	0	1	mammals	0	1	Micro	INT
Anaplasma.phagocytophilum	Anaplasma	Anaplasmataceae	0	0	ticks	0	0	1	1	Micro	BL
	Anaplasma	Anaplasmataceae	0	0	ticks	0	0	1	1	Micro	BL
Ehrlichia.canis	Ehrlichia	Anaplasmataceae	0	0	ticks	0	0	1	0	Micro	BL
	Ehrlichia	Anaplasmataceae	0	0	ticks	0	0	1	0	Micro	BL
	Neoehrlichia	Anaplasmataceae	0	0	ticks	0	0	1	0	Micro	BL
	Bartonella	Bartonellaceae	0	0	ticks	0	0	1	0	Micro	BL
	Chlamydophila	Chlamydiaceae	1	0	0	0	0	0	1	Micro	ALL
	Coxiella	Coxiellaceae	0	0	ticks	0	0	1	1	Micro	BL
Salmonella.enterica	Salmonella	Enterobacteriaceae	0	1	0	0	0	1	0	Micro	INT
	Leptospira	Leptospiraceae	0	1	0	0	0	1	0	Micro	RES
Mycobacterium.bovis	Mycobacterium	Mycobacteriaceae	1	0	0	0	0	0	1	Micro	RES

	Rickettsia	Rickettsiaceae	0	0	fleas, ticks	0	0	1	0	Micro	
	Borrelia	Spirochaetaceae	0	0	ticks	0	0	1	1	Micro	BL
Babesia.microti	Babesia	Theileriidae	0	0	ticks	0	0	1	0	Micro	BL
Babesia.vulpes	Babesia	Theileriidae	0	0	ticks	0	0	1	0	Micro	BL
	Babesia	Theileriidae	0	0	ticks	0	0	1	0	Micro	BL
		Cestoda	0	1	0	0	1	0	1	Macro	INT
Dipylidium.caninum	Dipylidium	Dilepididae	0	0	0	1	0	0	1	Macro	INT
Joyeuxiella.echinorhynchoides	Joyeuxiella	Dilepididae	0	0	0	2	beetles, rodents	0	1	Macro	INT
Diphyllobothrium.latum	Diphyllobothrium	Diphyllobothriidae	0	0	0	2	copepod - fish	0	1	Macro	INT
Alaria.alata	Alaria	Diplostomatidae	0	0	0	2	snails - frogs	0	1	Macro	INT
Hymenolepis.diminuta	Hymenolepis	Hymenolepididae	0	1	0	1	beetles, fleas	0	1	Macro	INT
Hymenolepis.nana	Hymenolepis	Hymenolepididae	0	1	0	1	beetles, fleas	0	1	Macro	INT
	Hymenolepis	Hymenolepididae	0	1	0	1	beetles, fleas	0	1	Macro	INT
Mesocestoides.lineatus	Mesocestoides	Mesocestoididae	0	0	0	0	0	0	1	Macro	INT
	Mesocestoides	Mesocestoididae	0	0	0	2	beetles, mites - vertebrates	0	1	Macro	INT
Echinococcus.multilocularis	Echinococcus	Taeniidae	0	0	0	1	rodents	0	1	Macro	INT
Taenia.crassiceps	Taenia	Taeniidae	0	0	0	1	rodents	0	1	Macro	INT
Taenia.hydatigena	Taenia	Taeniidae	0	0	0	1	mammals	0	1	Macro	INT
Taenia.ovis	Taenia	Taeniidae	0	0	0	1	mammals	0	1	Macro	INT
Taenia.pisiformis	Taenia	Taeniidae	0	0	0	1	mammals	0	1	Macro	INT

Taenia.polyacantha	Taenia	Taeniidae	0	0	0	1	mammals	0	1	Macro	INT
Taenia.taeniformis	Taenia	Taeniidae	0	0	0	1	rodents	0	1	Macro	INT
	Taenia	Taeniidae	0	0	0	1	0	0	1	Macro	INT
Ancylostoma.caninum	Ancylostoma	Ancylostomatidae	0	1	0	0	0	1	1	Macro	INT
	Ancylostoma	Ancylostomatidae	0	1	0	0	0	1	1	Macro	INT
Uncinaria.stenocephala	Uncinaria	Ancylostomatidae	0	1	0	0	0	0	1	Macro	INT
	Uncinaria	Ancylostomatidae	0	1	0	0	0	0	1	Macro	INT
		Ancylostomatidae	0	1	0	0	0	1	1	Macro	INT
Angiostrongylus.vasorum	Angiostrongylus	Angiostrongylidae	0	0	0	1	snails	0	1	Macro	RES
	Ascaris	Ascarididae	0	0	0	0	0	0	1	Macro	INT
Toxascaris.leonina	Toxascaris	Ascarididae	0	1	0	1	rodents	0	1	Macro	INT
Toxocara.canis	Toxocara	Ascarididae	0	1	0	0	0	0	1	Macro	INT
Crenosoma.vulpis	Crenosoma	Crenosomatidae	0	0	0	1	snails	0	1	Macro	RES
Dirofilaria.immitis	Dirofilaria	Onchocercidae	0	0	0	1	mosquitoes	0	1	Macro	HEA
	Trichostrongylus	Trichostrongylidae	0	1	0	0	0	0	1	Macro	INT
Dermacentor.reticulatus	Dermacentor	Ixodidae	1	1	0	0	0	0	1	Macro	SKN
	Ixodes	Ixodidae	1	1	0	0	0	0	1	Macro	SKN
Rhipicephalus.sanguineus	Rhipicephalus	Ixodidae	1	1	0	0	0	0	1	Macro	SKN
	Rhipicephalus	Ixodidae	1	1	0	0	0	0	1	Macro	SKN
	Ctenocephalides	Pulicidae	1	0	0	0	0	0	1	Macro	SKN
	pulex	Pulicidae	1	0	0	0	0	0	1	Macro	SKN
Sarcoptes.scabiei	Sarcoptes	Sarcoptidae	1	0	0	0	0	1	1	Macro	SKN
Capillaria.plica	Capillaria	Capillariidae	0	1	0	1	worms	0	1	Macro	BLAD
Capillaria.putorii	Capillaria	Capillariidae	0	1	0	0	0	0	1	Macro	ST
Eucoleus.aerophilus	Euculeus	Capillariidae	0	1	0	0	0	0	1	Macro	RES
Eucoleus.boehmi	Euculeus	Capillariidae	0	1	0	0	0	0	1	Macro	RES
	Euculeus	Capillariidae	0	1	0	0	0	0	1	Macro	RES
	Trichinella	Trichinellidae	0	0	0	1	host	0	1	Macro	INT
Trichuris.vulpis	Trichuris	Trichuridae	0	1	0	0	0	0	1	Macro	INT

	Trichuris	Trichuridae	0	1	0	0	0	0	1	Macro	INT
Pterygodermatites.affinis	Pterygodermatites	Rictulariidae	0	0	0	1	0	0	1	Macro	INT
Linguatula.serrata	Linguatula	Linguatulidae	0	0	0	1	mammals	0	1	Macro	RES
Molineus.legerae	Molineus	Molineidae	0	1	0	0	0	0	1	Macro	INT
Molineus.patens	Molineus	Molineidae	0	1	0	0	0	0	1	Macro	INT
	Echinostoma	Echinostomatidae	0	0	0	2	snails - frogs	0	1	Macro	INT
	Apophallus	Heterophyidae	0	0	0	1	fish	0	1	Macro	INT
Metorchis.bilis	Metorchis	Opisthorchiidae	0	0	0	2	snails - fish	0	1	Macro	LIV
Spirocerca.lupi	Spirocerca	Spirocercidae	0	0	0	1	beetles	1	1	Macro	HEA
Spirocerca.vulpis	Spirocerca	Spirocercidae	0	0	0	1	beetles	1	1	Macro	HEA
	Spirocerca	Spirocercidae	0	0	0	1	beetles	1	1	Macro	HEA
Strongyloides.stercoralis	Strongyloides	Strongyloididae	0	1	0	0	0	0	1	Macro	INT
	Strongyloides	Strongyloididae	0	1	0	0	0	0	1	Macro	INT
Oxynema.crassispiculum	Oxynema	Subuluridae	0	1	0	0	1	0	1	Macro	INT
	Brachylaima	Brachylaimidae	0	0	0	2	snails - snails	0	1	Macro	INT
		Trematoda	0	0	0	1	snails	0	1	Macro	INT
Enterocytozoon.bieneusi	Enterocytozoon	Enterocytozoonidae	0	1	0	0	0	1	0	Micro	INT
Giardia.lamblia	Giardia	Giardiidae	1	1	0	0	0	0	1	Micro	INT
	Giardia	Giardiidae	1	1	0	0	0	0	1	Micro	INT
	Leishmania	Trypanosomatidae	0	0	flies	0	0	1	1	Micro	LIV
Canine.adenovirus	Mastadenovirus	Adenoviridae	1	0	0	0	0	1	0	Micro	LIV
Canine.adenovirus.1	Mastadenovirus	Adenoviridae	0	1	0	0	0	1	0	Micro	LIV
Canine.adenovirus.2	Mastadenovirus	Adenoviridae	0	1	0	0	0	1	0	Micro	LIV
Canine.Distemper.Virus	Morbillivirus	Paramyxoviridae	1	0	0	0	0	1	0	Micro	ALL
	Parvovirus	Parvoviridae	0	1	0	0	0	1	0	Micro	INT

Appendix 5c

Non-layered maps of the gaussian random field mean (in red to purple) and SD (in grey to white) for the multi-species model (Figures A5.1 – A5.2) and the *E. multilocularis* model (Figures A5.3 – A5.4) presented in chapter 5.

Figure A5.5 also shows the discarded mesh initially made by using the European coastline.

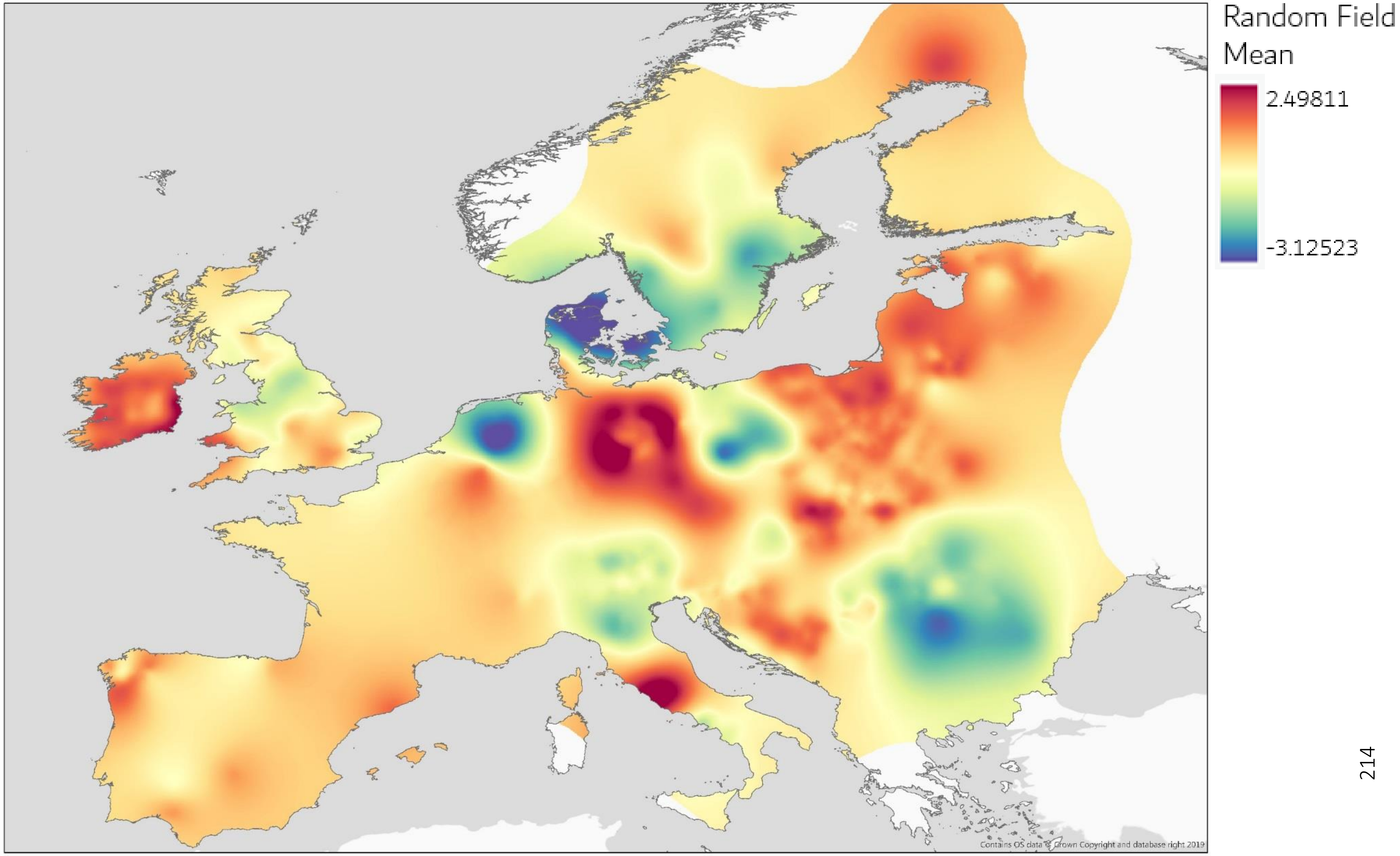

Figure A5.1 – Mean for Gaussian random field for the multi-species model presented in chapter 5.

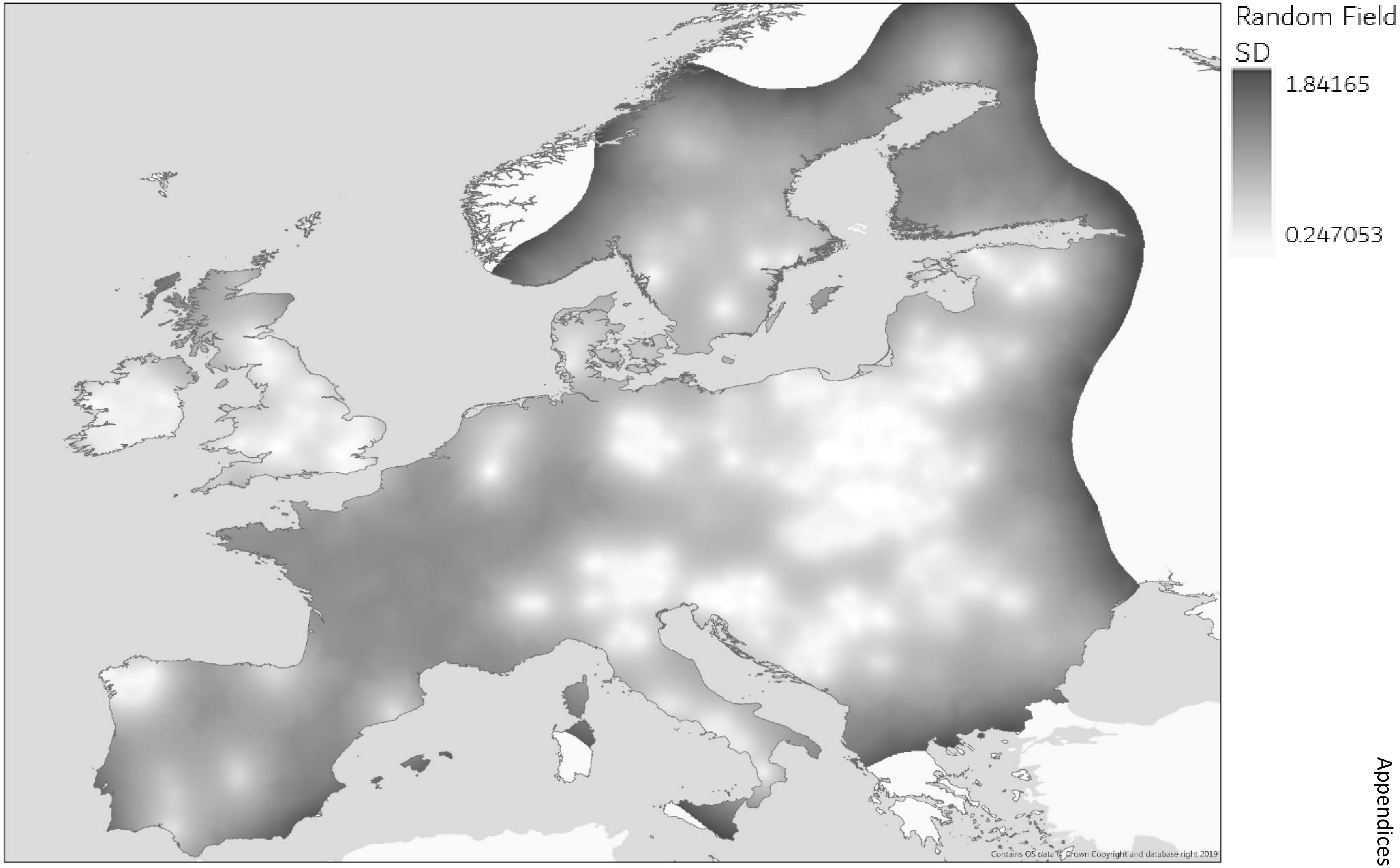

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Figure A5.2 – Standard deviation for Gaussian random field for the multi-species model presented in chapter 5.

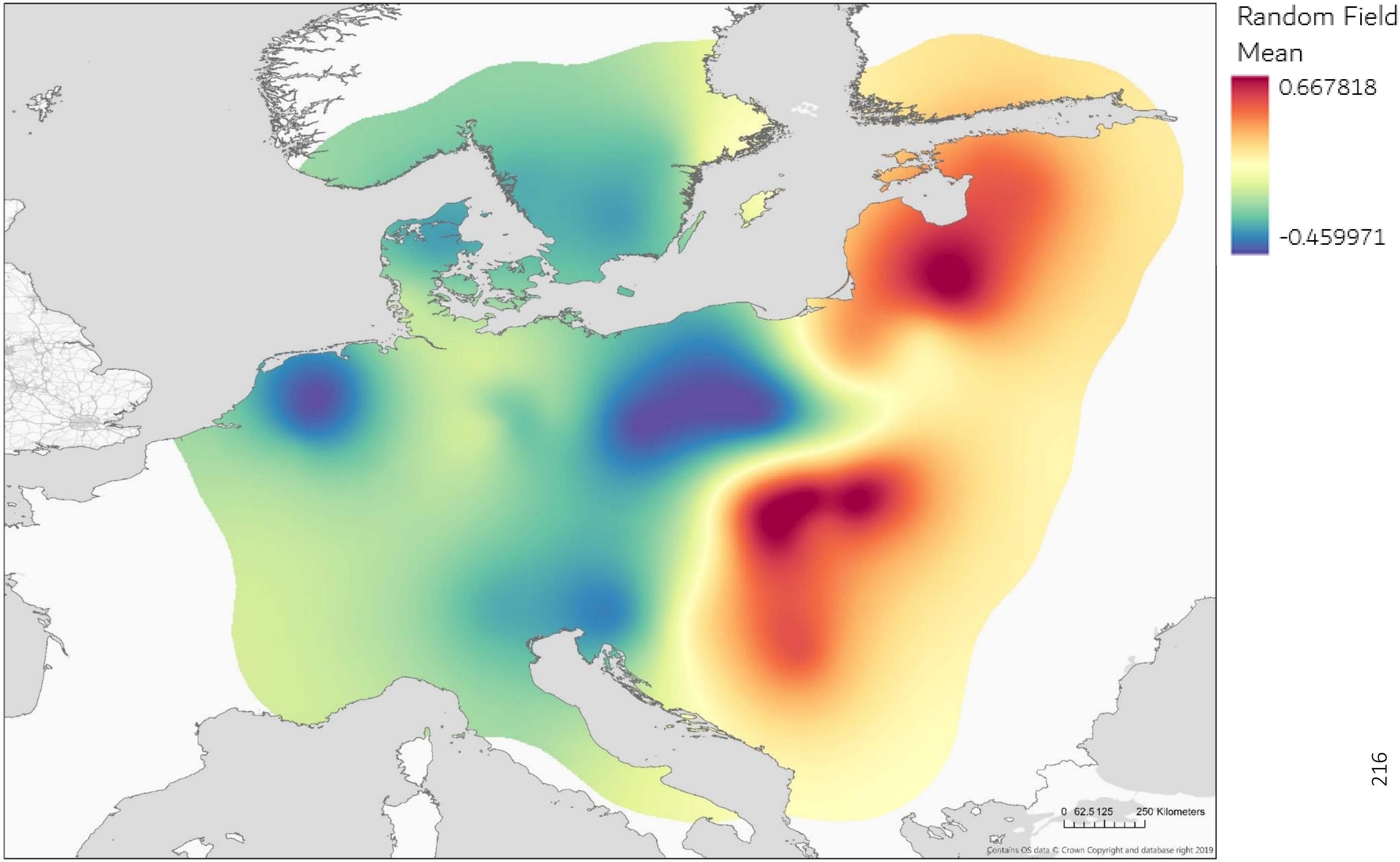

Figure A5.3 - Mean for Gaussian random field for the E.multilocularis model presented in chapter 5.

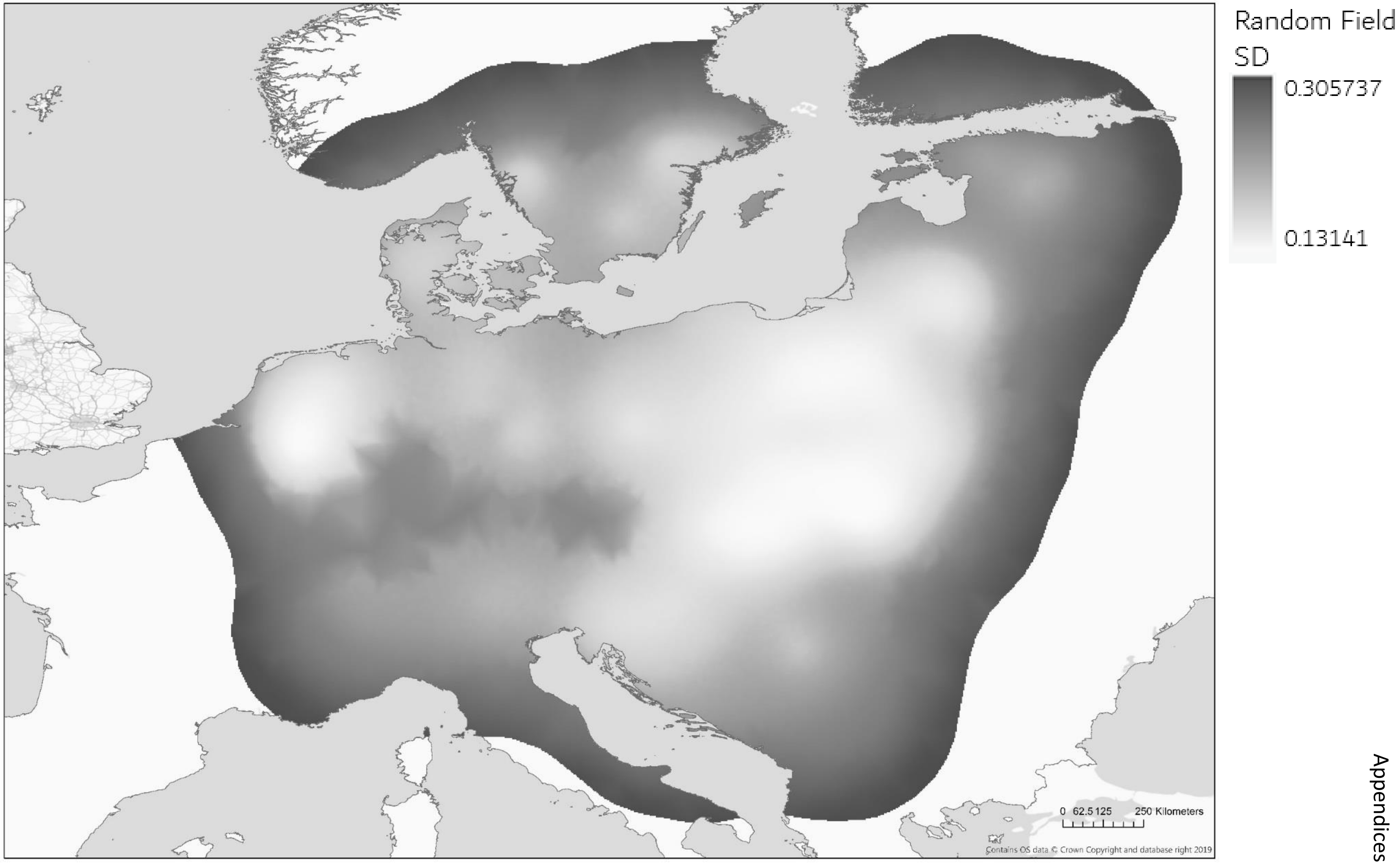

Figure A5.4 - Standard deviation for Gaussian random field for the E.multilocularis model presented in chapter 5.

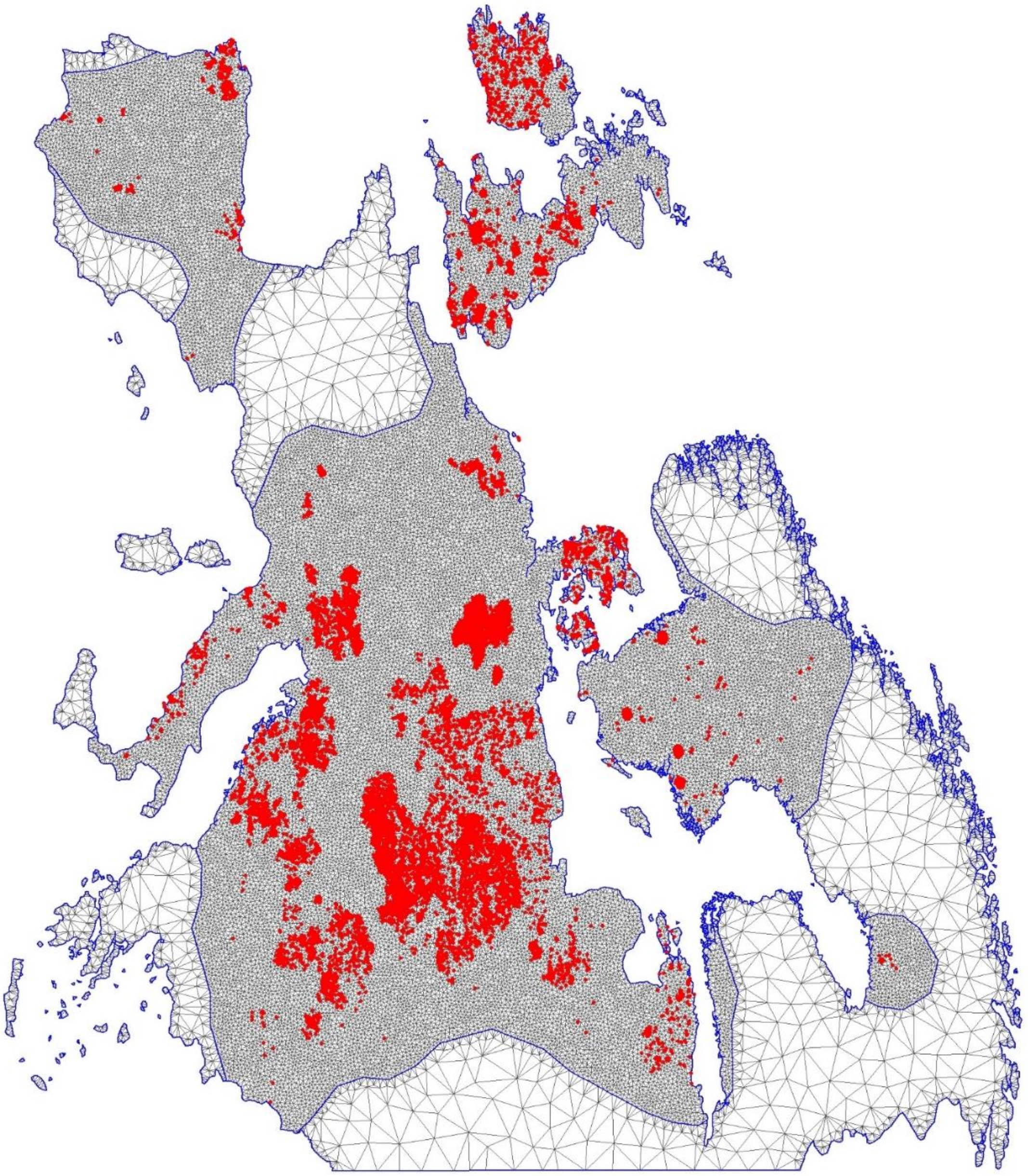

Figure A5.5 – Mesh initially constructed to fit the multi-species model presented in chapter5, including the Europe coastline.

Appendix 5d

Effects for each individual level of the three non-linear (iid) random effects included in the model: Detection method (Figure A5.6), Sample type (Figure A5.7) and parasite genus (Figure A5.8) .See Appendix 5b for the acronyms used to code sample and method.

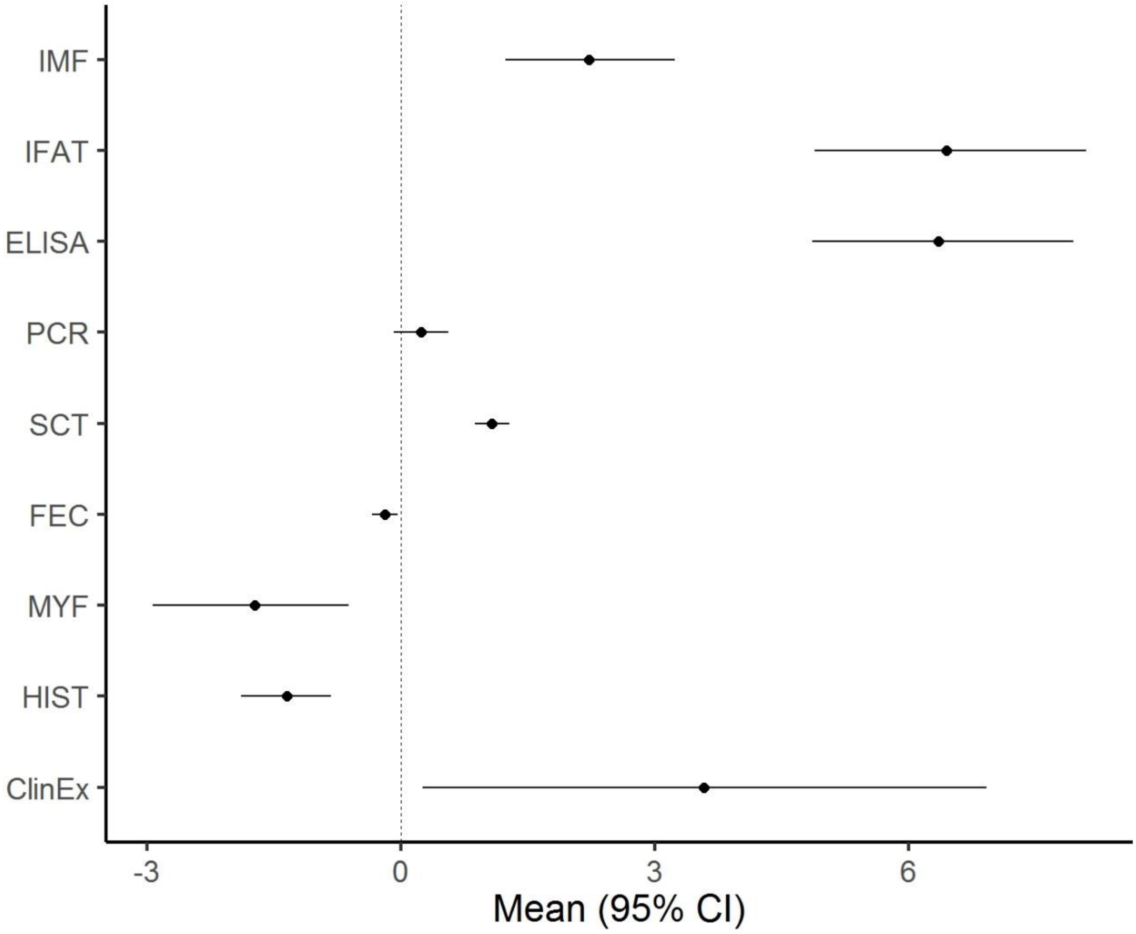

Figure A5.6– Individual effects of the levels for detection method included in the full model

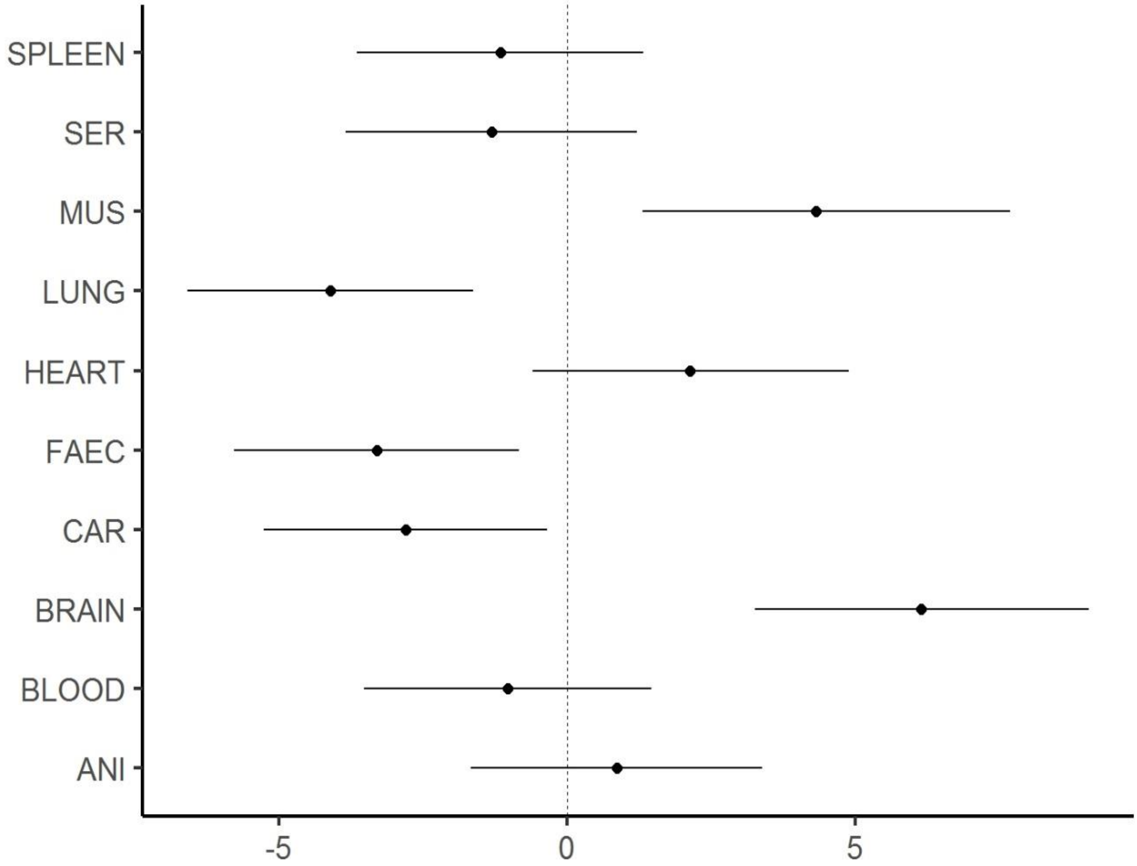

Figure A5.7 – Individual effects of the levels for sample type included in the full model

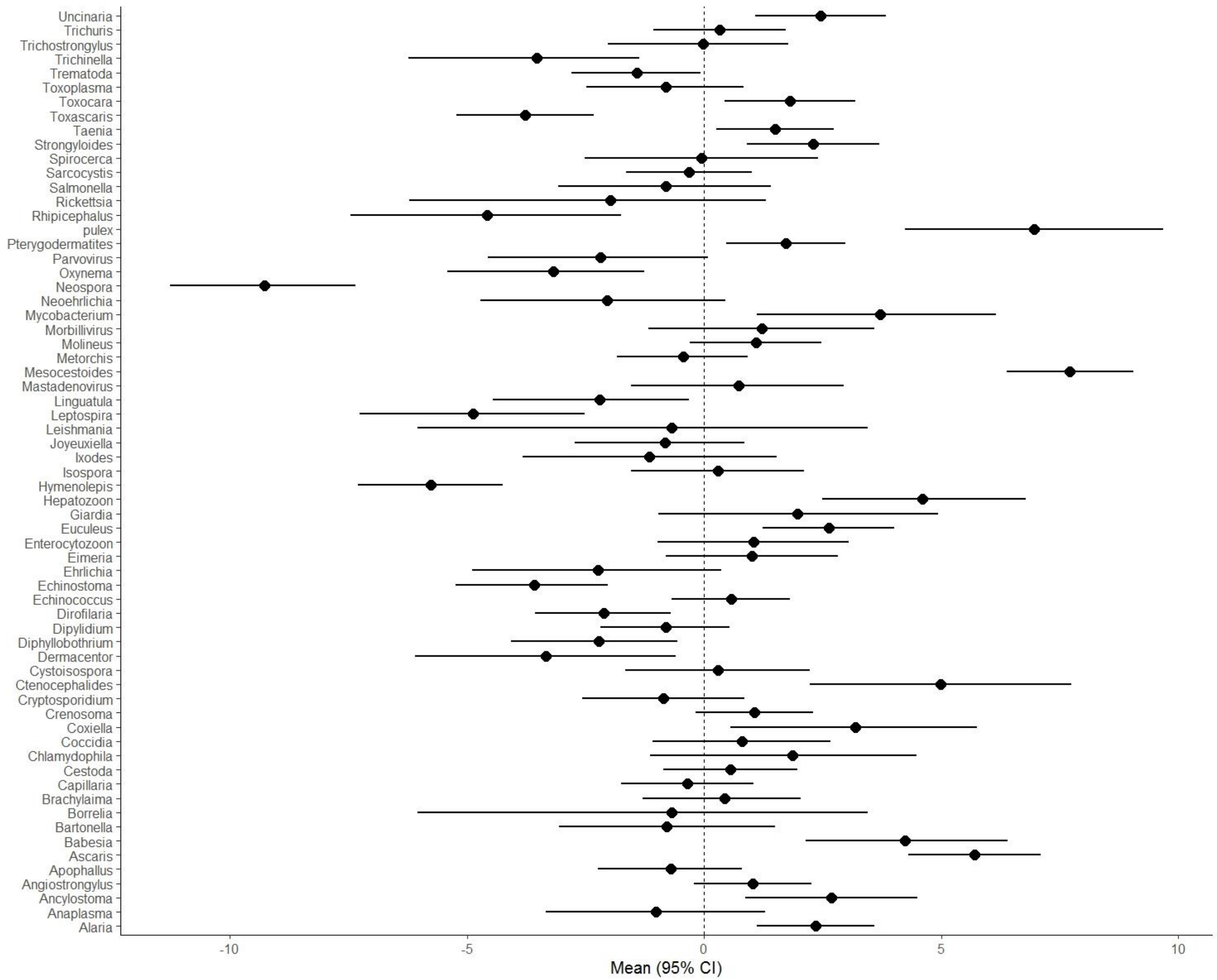

Figure A5.7 – Individual effects of the levels for parasite taxon included in the