Insect urban ecology: aphid interactions with natural enemies and mutualists

A thesis submitted by

Elise Amador Rocha

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School of Biological Sciences

University of Reading

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To Arthur

Declaration

I confirm that this is my own work and the use of all material from other sources has been properly and fully acknowledged.

Elise Amador Rocha

Reading, October, 2017

ABSTRACT

Cities are novel and fast changing environments. We have little understanding of how urbanisation affects ecological patterns and processes. In Chapter One I review the literature (with an emphasis on arthropods) concerning the general effects of urbanisation on biodiversity, how urban greenspaces are structured, the main characteristics of urban ecological populations and communities, and how trophic dynamics and species interactions are affected by urban environments. The experimental chapters of this thesis focuses on addressing gaps in knowledge concerning how species interactions respond to increasing levels of urbanisation, by using aphids and their natural enemies and ant mutualists as a model system. In Chapter Two I explore the local and fine scale environmental drivers of naturally occurring assemblages of aphids, and their coccinelid and syrphid predators, in urban gardens. Ladybirds are the only group affected by increased urbanisation, while aphids and hoverflies vary as a function of host plant abundance and garden plant richness, which in themselves are indirect consequences of urbanisation. In Chapter Three, I investigate the main biotic and abiotic factors that affect the recruitment of naturally occurring predators, parasitoids and mutualists in experimental colonies placed on an urbanisation gradient. In Chapter Four, I build on this to consider how two aphid species, each differentially attended by mutualists, are influenced by urbanisation. In both chapters I found a higher sensitivity of predators to increased urbanisation, while ants appear to particularly benefit from the creation of these novel habitats. In Chapter Five I explore if there is a differential response of predator functional groups to urban green spaces, and I confirm my hypothesis that specialist predators respond more strongly to increased abundance and size of green space in urban areas. In Chapter Six I investigate which features of urban habitats have a greater influence in the outcome of interspecific competition, and my results suggest that an increased abundance of ants in urban habitats may act in concert with abiotic features of urbanisation to affect the dynamics of competition synergistically. In the seventh and final chapter, I discuss the main findings, contributions and future directions in the field of urban ecology.

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Chapter 1 . INTRODUCTION

1.1 URBANISATION AND ITS EFFECTS ON BIODIVERSITY

Since the industrial revolution, human population growth and consequent urbanisation has negatively affected biodiversity, becoming one of the leading causes of species extinction (McKinney 2006, Hunter 2007, McKinney 2008). The growth of urban areas results in rapid changes on the landscape that may be considered permanent (Seto and Fragkias 2005, Bradley and Altizer 2007). Indeed, urbanisation causes a dramatic alteration on land structure characterised by dense housing, industries, roads and other associated infrastructure, mostly comprised of impervious surfaces. In addition to all these features, alterations that happen along urban gradients involve the loss and degradation of natural habitats, the introduction of exotic species, and microclimatic shifts (Bradley and Altizer 2007, Faeth et al. 2011).

Habitat alteration caused by urbanisation often exceed the habitat changes caused by farming and logging, since large areas of land are deforested, paved and radically restructured (Marzluff and Ewing 2001, McKinney 2006). This is due to the drastic physical changes caused by urbanisation. One commonly recognizable effect are the microclimatic shifts caused by the urban heat island effect, where city centres are shown to be much warmer than the surrounding non-urban matrix (Lo et al. 1997, Collins et al. 2000, Weng et al. 2004). There are also effects on soil chemistry, where high alkalinity is present, a result of the concrete and lime-base materials used in construction, which in turn could disfavour plants with high acidity requirements (Gilbert 1989). There are also the effects of eutrophication, altered atmospheric chemistry (sulphur oxides, $CO_{2,}$

aerosols, metals) and many other physical changes (Sukopp 2004, Kaye et al. 2006, Shen et al. 2008, McCarthy et al. 2010).

The disturbance created by the growth of urban areas not only damages the habitat of native species, but might also create novel habitats for species that are capable to adapt to these new conditions (McKinney 2006, Deguines et al. 2016). This process might promote biotic homogenisation, since it can replace native species by widespread generalist and non-native species on various spatial scales (McKinney and Lockwood 1999, McKinney and Lockwood 2001, Rahel 2002, Olden and Poff 2003, Olden et al. 2004, Douda et al. 2013, Concepción et al. 2015, Deguines et al. 2016). This alteration of the composition of wildlife communities can lead to biodiversity loss (McKinney 2002, Pauchard et al. 2006, McDonald et al. 2013) and increases in the abundance of species that can adapt to urban conditions (Sperry et al. 2001, Rickman and Connor 2003, Lessard and Buddle 2005). According to McKinney (2006) it is possible to categorize species along the urban–rural gradient: some species avoid urban areas and are extremely sensitive (urban avoiders), some species adapt really well to urban conditions, exploring and becoming dependent on urban resources (urban exploiters), and some species might adapt to urban habitats but utilize both natural and urban resources (urban adapters) (McKinney 2006). Understanding which factors are most important in differentiating how wildlife responds and adapts to urban conditions provides researchers with valuable opportunities for investigations into how selective and evolutionary processes can alter ecological interactions (Hunter 2007).

Arthropods are commonly used as bio-indicators of ecosystem health (Kremen et al. 1993, Gerlach et al. 2013, Burgio et al. 2015). There are great benefits of using arthropods when studying the effects of urbanisation on biological systems: they are diverse and may present an indication of biodiversity in an area; they hold a range of trophic functions (i.e. herbivores, predators, parasitoids, parasites, pollinators, detritivores, vector of diseases and mutualists); they are relatively easy to sample; they present short generation times which means they respond faster to changes in environmental conditions and experimental manipulations in comparison with other taxa, and they are crucial components of both natural and human-altered environments (McIntyre 2000, Bang and Faeth 2011, Van Nuland and Whitlow 2014).

The study of arthropods in urban environments provides a valuable opportunity for research, since urbanisation is considered an important cause for declines in arthropod populations (Pyle et al. 1981, Jones and Leather 2012, Baldock et al. 2015, Youngsteadt et al. 2017). According to McIntyre (2000), arthropods might respond directly through direct mortality caused, as an example, by increases in pollution and alterations in microclimate. They may also respond indirectly to alterations in the structure of their habitat, such as through a reduction in the abundance of key resources (e.g. host plants, oviposition and nesting sites), and mediation by altered interactions with natural enemies, competitors and mutualists. Individuals might suffer both direct and indirectly, with sensitive taxa strongly affected, and these effects might scale-up to changes in populations numbers and even community assembly (Pyle et al. 1981, McIntyre 2000).

The main characteristics of urban environments that can influence arthropods include bottom-up factors such as changes in resource quality and availability, and top down-factors such as natural enemy diversity and abundance (Thomas 1989, Kim 1992, Shrewsbury and Raupp 2006, Raupp et al. 2010, Burkman and Gardiner 2014). Nevertheless, recent studies are demonstrating that the effects of urbanisation might be harder to perceive and examine. Some investigations find no effect of urbanisation on the diversity of arthropods (Alaruikka et al. 2002, Faeth et al. 2011, Wojcik and McBride 2012), whereas others show variation among both different habitats and taxonomic levels (Bang and Faeth 2011, Van Nuland and Whitlow 2014, Vergnes et al. 2014). As an example, urbanisation sometimes show no effect on richness on ground and rove beetles, however, native species might be substituted by generalist widespread species that are able to adapt to these new conditions (Niemelä et al. 2002, Venn et al. 2003, Deichsel 2006). There are often studies with opposing results (Faeth et al. 2011). For example some studies of the diversity of butterflies (Clark et al. 2007, Ramírez Restrepo and Halffter 2013), ground beetles (Sadler et al. 2006, Magura et al. 2010), ants (Holway and Suarez 2006, Thompson and McLachlan 2007, Uno et al. 2010) and parasitic Hymenoptera (Bennett and Gratton 2012) have demonstrated that diversity decreases with urbanisation. In contrast, others report the opposite: Lessard and Buddle (2005) (ants), Fortel et al. (2014) (bees), Magura et al. (2004) (carabid beetles). Most of the time the literature is unable to determine patterns behind process, therefore the dynamic of populations and the assembly of communities in urban habitats continues to be insufficiently understood (McDonnell and Pickett 1990, McIntyre 2000, Faeth et al. 2005, Raupp et al. 2010).

Urbanisation has never occurred in such large scales, and a key threshold was passed in 2008, when for the first time in history more than 50% of the human population lived in cities and urbanised environments (Goddard et al. 2010, Buhaug and Urdal 2013).

It is estimated that the global human population of 7.2 billion in 2013 will reach more than 8 billion in the next twelve years, and further increasing to 10.9 billion people by 2100 (DESA 2013). Although urban areas are not a large portion of the Earth's land (~4% globally), the dramatic effects of urbanisation extends across and outside cities' limits and cause environmental changes at various scales (Grimm et al. 2008). The loss and degradation of habitats are accepted as one of the main causes of wildlife declines, which will heavily impact ecological processes (Goddard et al. 2010). The creation and growth of urban areas influences the surrounding landscape through fragmentation and isolation of habitats, changes in local and regional climates, introduction of invasive species, pollution, and alteration of biogeochemical cycles (Grimm et al. 2008, Bang and Faeth 2011). Understanding how biodiversity will respond to urbanisation is extremely important to provide guidance for future conservation planning, and ecologists should recognise that the creation of novel habitats provided by urban areas offers a great opportunity to answer these questions.

1.2 URBAN GREENSPACES AND GREEN INFRASTRUCTURE

Urban green space is a crucial element of cities, and provides a variety of ecosystem services to those who live in urban environments (James et al. 2009), and can be described as any area containing vegetated land or water within a city. The amount, composition, location and structure of green spaces in cities will determine their quality and ecological functions (Pauleit and Duhme 2000, Whitford et al. 2001, Turner et al. 2005). These functions and services include the provision and sustenance of ecological processes such as plant pollination, pest suppression, population dynamics and community resilience (James et al. 2009, Bennett and Lovell 2014). Urban green spaces can also provide crucial environmental services such the reduction of carbon emissions and air pollution (Hutchings et al. 2012, Strohbach et al. 2012); rainwater drainage (Bolund and Hunhammar 1999, Mentens et al. 2006); the regulation of air temperature and microclimates (Shashua-Bar and Hoffman 2000, Millward and Sabir 2011); and supporting bio-physical process (e.g. decomposition and soil formation, James et al. 2009, Gómez-Baggethun and Barton 2013).

A great part of the ecological research made in cities is about seeking associations between species richness and/or diversity and cities' features. For example, the abundance of plant species in urban areas generally positively relates with the size of human populations, and this correlation appears to be even stronger than the correlation with the total area of the city studied (Pickett et al. 2001). This relationship might be caused by the presence of non-native plant species. In general, the number of non-native plants in an area increases with stronger urbanisation levels (McDonnell and Pickett 1990, McIntyre 2000, Walker et al. 2009), which could negatively affect native herbivores present in the same area (Tallamy 2004, Burghardt et al. 2009). This alteration in plant communities may influence herbivorous arthropods regarding temporal variation in their food resources, nest and oviposition sites, shelter, and the presence and distribution of their natural enemies (Shrewsbury and Raupp 2006, Smith and Fellowes 2014, 2015). Across urbanisation gradients, herbivore diversity can be directly linked to plant distribution, identity and structure (Raupp et al. 2010).

Urban greenspaces are highly variable among cities, but usually consist of non-paved areas with some vegetation cover, such as domestic and community gardens, public parks, cemeteries and churchyards (Burkman and Gardiner 2014). The phenology of urban plants can be different from those found in rural areas; the literature review of flowering phenology made by Neil and Wu (2006) in urban environments indicates that plants that generally bloom in spring in a variety of ecosystems in Europe, North America and China are blooming earlier in urban environments than in other habitats. Such changes could be caused by shifts in local climate caused be the urban heat island effect (Pickett et al. 2011), where differences in air temperature between cities and their surrounding rural regions are observed (Weng et al. 2004). In addition, an important characteristic of urban vegetation is its spatial heterogeneity, which is created by a variety of different land uses, buildings types and social contexts (Pickett et al. 2011). The importance of these elements for urban populations and communities has already been recognized (Hanski 1998, Loreau et al. 2003, Burkman and Gardiner 2014).

Urban green spaces can also help to conserve biodiversity, supporting a large number of species: a national survey about the tree diversity in 147 towns in the UK showed that residential areas with medium and lower house densities showed the greatest species richness (about 234 species), and about of 50% of the surveyed sites had 10 and 50 trees or shrubs/ha. In addition, the survey showed that most trees and shrubs were found mainly in private gardens or on less accessible land (e.g. churchyards, schools, etc.). Open space and public parks had 20% of trees and shrubs and 12% were located bordering streets or highways (Britt and Johnston 2008).

Domestic gardens are the most important component of urban green space (Smith et al. 2006b). According to Gaston et al. (2005), domestic gardens occupy 19–27% of the entire UK urban area. Private gardens have been shown to have high levels of plant and animal species richness (Rudd et al. 2002, Thompson et al. 2003, Pauleit et al. 2005, Barratt et al. 2015), and yet only few studies have examined what are the implications of habitat differences in gardens for predation services (e.g. Burkman and Gardiner 2014, Philpott and Bichier 2017), as well as patterns of community structuring and function of both herbivores and natural enemies – but see Gardiner et al. (2014) and Burks and Philpott (2017). In addition to these gaps in scientific knowledge, there is also a gap in knowledge of the practical management of urban greenspaces, such as how to control pest populations, and how to inform urban farmers and gardeners about management and decision practices that can affect biodiversity and ecosystem services (Aronson et al. 2017, Philpott and Bichier 2017).

1.3 URBAN POPULATION DYNAMICS

Urban environments are made of complex landscapes, and the characteristics of these areas might affect the dynamics of the populations present (Anderies et al. 2007). Therefore, cities may offer great research opportunities for comparative studies as it provides a suite of habitats with fast changing environmental conditions, both at local and at regional scales (Collins et al. 2000, Grimm et al. 2000, McKinney and Lockwood 2001). Although urban and suburban habitats might present high stress to some sensitive species, they sometimes harbour high resource abundance, by providing non-native host plants for endemic herbivores (Connor et al. 2002, Anderies et al. 2007). The difference between population numbers in urban areas in comparison with more natural habitats may follow the predictions made by Parker (1978), where the increase in the amount in resource density will lead to an increase in population density as well. Indeed, high densities of certain herbivorous arthropods have been documented in urban forests, whereas in natural forests they rarely reach such high numbers (Dreistadt et al. 1990, Hanks and Denno 1993, Watson et al. 1994, Tooker and Hanks 2000). In their work, Graves and Shapiro (2003) detected that about 34% of California butterfly species are using nectar resources and ovipositing on non-native plant species, which caused some species to increase their geographic range.

However, is important to note that not all species and populations will follow this trend, although there is a conventional belief that urban areas harbour lower diversity (i.e. lower richness and evenness of species), while abundances is thought to increase (probably due to higher habitat productivity) (e.g. Marzluff and Ewing 2001, Chace and Walsh 2006, Grimm et al. 2008, Shochat et al. 2010), through a meta-analysis Saari et al. (2016) found that the general abundance of species was actually lower in urban areas, and lower species richness could not be confirmed.

Therefore, is important to consider that the increased habitat productivity might benefit some species more than others, which in turn might indirectly lead to increased competitive exclusion in these areas (Shochat et al. 2004a). In addition, with the increase of habitat productivity, there is less temporal variation in cities when compared to other habitats (Catterall et al. 1998, Beckmann and Berger 2003), generally because urban management schemes result in resources being available at an artificially constant level. Consequently, only certain species benefit from this reduced temporal variability, which might explain the high population numbers of some native species (Shochat et al. 2006). On the other hand, some rarer and specialised species could be less successful indicating that they are more likely to become extinct in these habitats since they probably would not be able to reach the numbers necessary to sustain a resilient population. Denys and Schmidt (1998) found that there was a decline in parasitoid species numbers along an urbanisation gradient stronger than the decline in generalist predatory species numbers. The percentage of parasitism declined significantly with increasing habitat isolation, while predator-prey ratios did not show the same trend. This was most apparent for rare parasitoids species, which showed even lower species numbers.

As cities expand, fragments of natural habitat tend to become progressively smaller, and the distance between fragments increases. The isolation and distance between patches might lead to a reduced population movement and consequently also decreased gene flow, this process therefore might disrupt a population into several smaller subpopulations (Bierwagen 2007, McDonald et al. 2013). Both intergenerational and seasonal migration might also be impaired, however good dispersers might be less affected in comparison to less mobile species (Saunders et al. 1991, McDonald et al. 2013). According to Concepción et al. (2015), is important to also consider the interaction between species mobility and habitat specialization, because specialist mobile species might be greatly affected by urbanisation since highly mobile species generally have larger geographic ranges, and as a result might be more sensitive to the increased habitat patchiness in larger spatial scales (Thomas 2000, Chace and Walsh 2006, Slade et al. 2013).

Urbanisation can also alter the phenology and behaviour of some species in cities (Neil and Wu 2006, Shochat et al. 2006, Lowe et al. 2017). These changes have the potential to drive large differences among populations, depending on whether these changes are positive or negative for the species which is being examined (Rodewald et al.

2011, Lowe et al. 2017). As an example, changes in emergence time or migration could allow species living in urban areas to take advantage of resources that are already available and on which normally they do not feed upon (Lowe et al. 2017). Altered life cycles could be advantageous for urban-tolerant species if their peak abundance times become disassociated from those of their natural enemies, but could also cause a disadvantage if individuals no longer emerge at the same time as their main resources (Neil et al. 2014, Meineke et al. 2014, Nelson and Forbes 2014, Lowe et al. 2017). Consequently changes on species' traits or phenology of species living in urban areas could be contributing to their success in these environments (Lowe et al. 2017).

Habitat selection and suitability is traditionally considered as a result of animals selecting where to live, as a consequence of behaviours linked to movement and dispersal (Moorcroft and Barnett 2008, Rebolo-Ifrán et al. 2017). However, species respond not only to habitat patchiness, but also to processes that can create heterogeneity in the distribution of ecological conditions (e.g. microclimates, soil, topography, vegetation cover, food availability, competition, predation) that will influence individual's fitness and adaptation (Sutcliffe et al. 1997, Meineke et al. 2013, Stein et al. 2014), so habitat selection patterns can also be a consequence of differences in the ability of a species to adapt (or not) to certain habitat types (Rebolo-Ifrán et al. 2017). In reality, the influences of abiotic factors of urban environments on arthropods, such as rainfall, the urban heat island effect, noise and artificial lighting, pollution and humidity, and biotic (e.g. predation, parasitism, plant diversity) still need to be fully examined (Dale and Frank 2014). According to McGill et al. (2015), we still need a better understanding of how individuals (winners and losers) are influenced by various human impacts and how they scale up to populations and overall community trends in biodiversity. With losers being considered species that are decreasing in their abundance, range, and/or occupancy through time, the extreme being extinctions (e.g. urban avoiders, McKinney 2006). Conversely, winners are species that are increasing in their abundance, range, and/or occupancy through time, the extreme being globally invasive species (McGill et al. 2015, Rebolo-Ifrán et al. 2017). As human populations continue to modify natural habitats, it is important to understand how anthropogenic disturbance affects urban populations in order to predict and hopefully mitigate significant negative effects to the function of urban ecosystems (Lowe et al. 2017).

1.4 URBAN COMMUNITY STRUCTURE

Urban ecosystems are characterized by high human population densities and associated infrastructure that meet the human population needs (Pickett et al. 2011). Although progress and associated technologies have increased our perception of an urban society that is separated from nature, the demands placed on ecosystem services keeps increasing progressively (Gómez-Baggethun and Barton 2013). Biological communities living in urban habitats might be radically altered in terms of diversity, composition and trophic structure in comparison to other natural habitats (Shochat et al. 2010, Saari et al. 2016). In comparison to rural areas, species richness found in cities may actually be higher, depending on the initial local and regional pool of species previously present, however, global species richness generally declines with increasing urbanisation (McDonald et al. 2013). Species composition in urban environments might depend on the presence of many habitat types (e.g., ornamental plants, gardens, lawns, meadows, bushes, ponds etc.), built structures (buildings, roads and other paved areas), topography, microclimate, pollution, and traffic (Sattler et al. 2010a). The increase in habitat patchiness and reduction in availability of key resources might result in loss of species (Didham et al. 1996, Harrison and Bruna 1999).

Patch size in urban environments influences species richness and species composition, with organisms at higher trophic levels being those more negatively affected by smaller habitat patches (Gibb and Hochuli 2002, Bennett and Gratton 2012, Pereira-Peixoto et al. 2016). Wildlife present in the world's cities is said to become progressively more similar and homogenised, in comparison to the species composition present prior to urbanisation (Pyšek et al. 2004, Hobbs et al. 2006, Grimm et al. 2008, McDonald et al. 2013). For plant communities, Ramalho et al. (2014) demonstrated that land fragmentation can have complex effects in plant communities, which suffer impacts faster in smaller remnants. These smaller patch sizes lost half of their plant richness in a few decades, while large remnants maintained higher diversity. How these trends in plants communities will scale-up on communities of arthropods it is still a matter for further investigation.

Different cities may sometimes present similarities in species composition, and this process is hypothesized to be due to the transportation of similar groups of species (e.g. plant trade), and also through similarities in spatial structure of cities which lead to analogous sets of species being able to adapt to both biotic and abiotic conditions (McKinney and Lockwood 1999, McKinney 2006, Pickett et al. 2011). Connectivity is an important factor in structuring urban communities, in the work performed by Vergnes et al. (2012) the community composition of staphylinid beetles, carabid beetles, and spiders in domestic gardens showed that the diversity of these groups that are closer to woody corridors are more similar to large woodlands in comparison to other sites, and the authors concluded that resource availability and habitat connectivity are major factors determining the composition of these communities. Increased habitat heterogeneity has been show to benefit generalist herbivorous species (Sattler et al. 2010b), while natural enemies, specially parasitoids, might present decreased numbers in isolated patches (Denys and Schmidt 1998). These patterns confirm the consensus that across urban habitats and urbanisation gradients, habitat specialists might benefit from higher connectivity between greenspaces (Burkman and Gardiner 2014, Rossetti et al. 2017).

Although there is a great deal of studies reporting patterns of community composition and diversity related to urbanisation, only a few have actually engaged to explain processes behind patterns. As an example, few studies have addressed how the intensity of human activities (e.g. pest management, traffic), landscape dynamics and structure (e.g. patch size, isolation, edge area, time since isolation) and local environmental conditions might determine and affect local population dynamics, and the consequent changes to community structure in urban areas (Ramalho et al. 2014). Developing proper knowledge about how habitat degradation and associated fragmentation affect urban ecosystems has proven to be difficult and challenging, and the challenge arises from the multiple complex ways that landscapes change following creation of cities potentially impacts communities of interacting species (Brudvig et al. 2015).

It is assumed that the processes that dictate community assembly depend on species' characteristics and traits, such as their degree of resource specialisation and dispersal abilities, and also their interaction, which is generally not taken into consideration in most studies (but see Concepción et al. 2015). It is considered that processes known as environmental filtering might exclude species from occurring in certain habitats, mainly because their resource requirements are not met; on the other hand, biotic filtering or limiting similarity might prevent species from occurring in certain places due to displacement by stronger competitors (Mason et al. 2005, Grime 2006, Mouillot et al. 2007, Concepción et al. 2015). Every species has its own set of functional traits and will respond accordingly to habitat alteration that characterizes urban habitats (McIntyre et al. 2001, Fortel et al. 2014). This way, specialist species with narrow ecological niches and poor dispersal abilities would probably be much more affected by habitat patchiness and degradation than generalist species (Öckinger et al. 2010, Concepción et al. 2015). Furthermore, these processes that dictate community dynamics and assembly are most certainly scale dependent and might act with higher intensity in fast changing environments (Mason et al. 2011, de Bello et al. 2013, Concepción et al. 2015). This multitude of species responses to habitat alterations and fragmentation make predictions about community dynamics and assembly in urban habitats extremely challenging to predict. However, some studies that focused on different processes responsible to determine the community assembly and dynamics of arthropods in cities have appeared lately (Braaker et al. 2014, Bogyó et al. 2015, Concepción et al. 2015, Braaker et al. 2017). In order to guide future research effort that look to elucidate processes behind the ecological patterns in urban communities, Aronson et al. (2016) suggested using a series of hierarchical filters that might influence species occurrences and distributions in cities as a “conceptual framework”. These filters represent anthropogenic, biotic and environmental aspects of cities that determine species composition in various spatial scales like human mediated biotic interchange and introductions, climate and biogeography, cultural and socioeconomic factors, urban structure and history of development and species interactions (Aronson et al. 2016).

1.5 URBAN TROPHIC DYNAMICS AND SPECIES INTERACTIONS

As the world becomes more urbanised, it's imperative that we understand the structure and function of food webs in urban areas (McKinney 2002, Faeth et al. 2005). As cities spread and urbanisation intensifies, invasive widespread and generalist species might displace native ones when competing for resources, which might lead to extinctions of native species and elevated numbers of "stronger competitors" and species that can adapt to these altered new habitats (Pickett et al. 2011, McDonald et al. 2013). The functioning of ecosystems rely on the resilience of arthropod communities, which play important roles in ecological services, and as shifts and replacement are made in community composition, ecosystem functioning in these areas might be substantially affected (Bolger et al. 2000, Niemelä et al. 2000, McIntyre et al. 2001, Ryall and Fahrig 2005, Christie et al. 2010). Changes in community dynamics and structure might arise from trophic cascades, for example by following extinctions of species at higher trophic levels influencing those groups that belong to basal trophic levels (i.e. "top-down" effects) (Ricketts and Imhoff 2003, Christie et al. 2010).

Consequently, resource controlled food webs might not be strongly affected if a predator becomes extinct; however a similar loss in a system that is mainly controlled by top-down forces might suffer alterations in ecosystem function and stability (e.g. pest regulation, nutrient cycling, pollination) (Faeth et al. 2005). Regulation by top-down forces generally means that the main cause of mortality of an herbivore is caused by predation, although is important to consider that herbivore suppression is not necessarily density dependent (Letourneau et al. 2009). The efficiency of natural enemies in regulating herbivore populations is said to affect crop production, productivity, plant processing rates and nutrient cycling (Parish et al. 1999, Schmitz 2007, Letourneau et al. 2009).

The fragmentation of habitats, which typically occurs in urban areas, might affect insect richness and evenness, and also their interaction with other species and trophic groups (Didham et al. 1996). As an example, shifts in proportion of specialist/generalist natural enemies in relation to the range of prey available might be affected by habitat fragmentation and connectivity (Webb and Hopkins 1984, Kruess and Tscharntke 1994, Gibb and Hochuli 2002). However, specialists might be less successful at adapting to new environmental conditions in comparison to invasive and widespread generalist species (Didham et al. 1996, Concepción et al. 2015). Shrewsbury and Raupp (2006) found that residential areas with more complex plant structures maintained higher numbers of generalist predators. The authors hypothesised that higher numbers of generalist predators also increased pest regulation and control of lace bugs in these areas, which are the most important prey of this group. Other studies have also documented urban habitats with higher structural complexity supporting higher species numbers and abundances of generalist predators (Hanks and Denno 1993, Tooker and Hanks 2000, Frank and Shrewsbury 2004, Shrewsbury et al. 2004, Sorace and Gustin 2009, Gardiner et al. 2014). Structural diverse and complex habitats are thought to provide alternative food sources and prey, nest and oviposition sites, favourable microhabitats and shelter (Landis et al. 2000, Langellotto and Denno 2004).

However, increased human activities that create urban habitats with a poor structural complexity (e.g. fewer green spaces, poor plant species richness, no temporal variability) can cause a reduction of top predators, which may in turn affect food web structure due to altered trophic cascades (Faeth et al. 2005). As successional changes occur, alterations of species composition, particularly in predator and natural enemies groups, might affect the control of trophic structure and food web dynamics in cities (Collins et al. 2000, Faeth et al. 2005). Understanding how species interactions and the assembly of communities in these highly complex landscapes is still a matter of constant investigation; nevertheless is important to recognise that all communities are formed from the species pool present, at any given spatial scale. In the work performed by Aronson et al. (2016), three main species pools were identified as being affected by urbanisation: the regional, city, and local pools. The pool of a certain region is formed by all species within a greater geographic region surrounding a particular city. The city pool contains a subset of species that were already present in the regional pool and are able to live in urban conditions. The local pool is where the species from the city pool were filtered and exist within a fine scale location (e.g. garden, park). The local pool is predominantly where interactions between species occur, and therefore is the preferred scale choice where researchers must focus when looking to understand how species composition and food web dynamics happen both in urban and other habitat types (Aronson et al. 2016). Predator occurrence and abundance can change across habitats, so variation in predation risk might create heterogeneous “landscapes of fear” consequently influencing patterns in habitat selection (Carrete et al. 2009, Laundré et al. 2014, Rebolo-Ifrán et al. 2017). As predators generally show to be more sensitive than their prey to urbanisation, some species might benefit from the relaxed predation pressure in some areas, and consequently could preferentially select urban environments (Berger 2007, Shannon et al. 2014, Rebolo-Ifrán et al. 2017).

However, it is challenging to understand the importance of top-down control in urban habitats without knowing with a certain degree of detail about the individual responses of both prey and predator species to these same habitats (Patten and Bolger 2003). Also, although the top-down regulatory mechanism performed by predators is commonly cited to explain the dynamics of natural populations (Erlinge et al. 1983, Hanski et al. 2001, Terborgh et al. 2001), the actual consequence of this effect on population abundances is controversial (Ballard et al. 2001, Meserve et al. 2003, Previtali et al. 2009, Rebolo-Ifrán et al. 2017). Mutualism and competition are other regulatory mechanisms that are often not considered as factors potentially determining population and community dynamics, and might also present heterogeneity in the magnitude of effects across landscapes (Laundré et al. 2014, Rebolo-Ifrán et al. 2017). Two species directly interacting in a community can create habitat heterogeneity indirectly to another species, as detected by Liere et al. 2014, which studied the system of the predacious beetle *Azya orbigera*, which mainly feeds on the hemipteran *Coccus viridis,* which is ant attended by the tree-nesting ant *Azteca instabilis* (Hymenoptera: Formicidae). The beetle presents life-stage dependent vulnerability, being the larvae immune to ant attacks, while the adult is heavily attacked by *A. instabilis*. This differential vulnerability to ants creates two habitat types that are utilised differently by *A. orbigera* larvae and adult, and therefore only plants around nests of *A. instabilis* present high populations of *C. viridis* (Liere et al. 2014). Chamberlain et al. (2014) through a meta-analysis that quantified variation in species interaction outcomes (competition, mutualism, or predation), found that both the magnitude and sign of species interactions varied the most along spatial and abiotic gradients. Moreover, still there are no studies that specifically tested how herbivore numbers, mutualism and predation concurrently behave and affect each other in response to variation and heterogeneity created by urban habitats.

In conclusion, spatial heterogeneity, biotic and abiotic features created by urbanisation are likely to be affecting trophic structure and food web dynamics in greater extent in cities in comparison to other environments (Faeth et al. 2005). On large time scales, alterations in species interactions can create variation in population numbers as well as in community dynamics, which might further alter food webs (Chamberlain et al. 2014). In fact, we still have a lot to learn about the complex ways predation, mutualism and competition occurring in novel ecosystems created by city growth might affect community assembly and dynamics in cities. In addition, understanding the responses of interactions between trophic groups in urban areas is crucial challenge that we must overcome in order to provide us with a better understanding of ecosystem services, as well as resilience to disturbance events (Christie et al. 2010), which only a few studies have started to investigate (e.g. Fenoglio et al. 2013, Geslin et al. 2013, Deguines et al. 2016, Turrini et al. 2016).

1.6 PURPOSE OF STUDY AND RESEARCH QUESTIONS

Increased anthropogenic alterations to ecosystems across the biosphere are impacting heavily the global biodiversity (Ellis et al. 2010, Newbold et al. 2015, Rebolo-Ifrán et al. 2017). Our ecological knowledge about cities is still far behind in comparison to other systems, and that is because there is a general notion that humans alter natural processes that scientific research is pursuing to understand. This way, biological systems in cities was long considered not worthy of ecological investigations (McDonnell and MacGregor-Fors 2016). Fortunately, ecologists have expanded their research possibilities and are recognizing the value of cities in providing us novel insights into ecological patterns and process that contribute to our ability to predict and mitigate potential impacts from future global development (Carreiro and Tripler 2005, Grimm et al. 2008, Youngsteadt et al. 2015). With the incredibly fast spread of urban areas, most of the time with lack of planning that ensure resilience of ecosystem functioning, we need a better understanding of the processes forming ecological communities present in cities (Aronson et al. 2016).

Urbanisation creates unique habitat structures and disturbance regimes, and contains assemblages of species that interact with each other in manners that we yet do not understand (Shochat et al. 2006, Martin et al. 2012, Youngsteadt et al. 2015). Moreover, these altered habitats can led to changes in migration patterns, habitat preference, reproductions rates and patterns of species interactions (Donnelly and Marzluff 2006, Turrini et al. 2016). As cities ages and succession occurs, these altered processes might cause evolutionary and phylogenetic changes that favour only a subset of well adapted species, which might lead to biotic homogenisation (Palumbi 2001, Wandeler et al. 2003, Faeth et al. 2011). In this context, the literature on biotic homogenisation suggests that cities might present similar species composition due to common features like amount of impermeable areas (buildings, roads), structure of green spaces (private and community gardens, parks), and similar disturbance rates from human activities (artificial lightning, noise, pollution) (Pyšek et al. 2004, Hobbs et al. 2006, Grimm et al. 2008, McDonald et al. 2013, Aronson et al. 2016). Nevertheless, each city is unique and generalisations must be carefully made taking in consideration factors such as culture, history, biogeographic region and socio-economics (McKinney 2006, Groffman et al. 2014, Parker 2015, Aronson et al. 2016).

With further creation and expansion of cities, we need to understand the complex ways wildlife might respond to altered biotic and abiotic conditions (Rebolo-Ifrán et al. 2017). Traditionally, urban ecology studies classified the urban matrix as broad habitat types (e.g. urban, suburban and rural areas) or only focused at large spatial scales that might distort and overly generalise differences among urban habitats (Ellis and Ramankutty 2008, Ramalho and Hobbs 2012, Savage et al. 2015). This way, we still have a lot to learn about fine scale drivers of urban biodiversity (McDonnell and Hahs 2013, Chown and Duffy 2015, Aronson et al. 2016). Fine-scale environmental factors might be more significant than landscape scale factors in influencing arthropod communities in cities (Savage et al. 2015, Aronson et al. 2016, Lowe et al. 2017), particularly processes that are mostly driven by species interactions. In this work, I wanted to contribute to reduce this lack of knowledge by focusing on local and fine scale environmental drivers of urban habitats in the interaction between herbivores, mutualists and natural enemies as well as drivers of species composition and dynamics in the assembly of herbivores and predators. We used aphids and their natural enemies and ant mutualists as a model system in our following experimental chapters. In Chapter 2, I investigated which characteristics of urban gardens determine species diversity and abundance of populations of naturally occurring aphids and its syrphid and coccinelid predators. I then examine how biotic and abiotic factors of urban habitats affects multitrophic interactions in experimental colonies placed on an urbanisation gradient, as well as aphid population size, natural enemies and mutualist occurrence (Chapter 3). Then I investigated how main urban habitat features (roads, buildings, gardens and plant diversity) might differentially affect aphid populations attended and not attended by mutualists, and the effect of ant occurrence on other predators of aphid species (Chapter 4). Next, I focused on the response of aphid predators' functional groups to the availability of green spaces within urban habitats (Chapter 5). Finally, in Chapter 6, I focused into more direct biological interactions, to see how interspecific competition between two closely related insect herbivores is affected by urbanisation.

Chapter 2 URBANISATION DIFFERENTIALLY INFLUENCES THE ABUNDANCE AND DIVERSITY OF APHIDS AND THEIR PREDATORS

2.1 INTRODUCTION

Urbanisation is perhaps the most extreme form of widespread anthropogenic habitat modification. Most environmental variables (e.g. climate, water flow, biological diversity) are greatly altered from what previously existed (Smith et al. 2006a). As a result, urbanisation can rapidly transform fundamental ecological processes (Goddard et al. 2010), which in turn alter ecological interactions at all trophic levels (Kaye et al. 2006, Shochat et al. 2006). Unsurprisingly, urbanisation is considered a significant driver of species extinctions (McDonald et al. 2008, Goddard et al. 2010), and represents a major proposed cause of insect decline (Jones and Leather 2012, Baldock et al. 2015).

However, the magnitude of the effects of urbanisation depends to a marked degree on the composition, amount and management of green spaces in cities (Marzluff and Ewing 2001, Loram et al. 2007). This is because urban green spaces can mitigate the detrimental impacts of urbanisation by providing ecosystem services and serve as refuges for plant and animal species (Goddard et al. 2010, Hennig and Ghazoul 2012). Domestic gardens are a major and important component of green spaces in urbanised areas (Smith et al. 2006a). In the UK, the amount of gardens in cities ranges from 35% in Edinburgh to 47% in Leicester (Loram et al. 2007). As habitats, gardens are maintained in a state of permanent succession, by the casual introduction of native plants (e.g. weeds and herbs), together with seasonal planned planting with frequent addition of new plants, coupled with other management decisions such as weeding, pesticide use and mowing (e.g. Smith and Fellowes 2014, Smith and Fellowes 2015). Overall, the composition of the garden flora tends to change each year, and the resulting plant diversity is high (Owen 1981). Therefore, gardens are thought to be vital in the sustenance of biodiversity in cities, however, diversity patterns of the different organism that inhabit gardens has still been little explored (Goddard et al. 2010). However, ecosystem functioning and ecosystem resilience depends not only of rich communities, but also fully functioning ecological processes (Hennig and Ghazoul 2012).

One process of great importance is top-down control, like the dampening of herbivore outbreaks, which is essential for food web stability (Faeth et al. 2005, Hironaka and Koike 2013). Urban environments often harbour large populations of herbivores that are considered pests, and their success arise from low natural enemy numbers, and also because management practices and vegetation structure benefits particular species of herbivores (Frankie and Ehler 1978, Barratt et al. 2015). Consequently, investigating herbivores and their natural enemies might help us to understand how variance in environmental factors affects trophic dynamics and consequently the function of urban ecosystems (Burkman and Gardiner 2014). Local and fine scale environmental factors are the main determinants of species interactions (Aronson et al. 2016), hence, comprehending those factors may provide us with proper knowledge that might help us to develop strategies that promote arthropod conservation and resilience of ecosystem services (Philpott et al. 2014).

Aphids are one of the few groups of insects that are more abundant in temperate regions than in the tropics (Brisson and Stern 2006). About 250 species feed and reach high population numbers on agricultural crops and cause an estimated hundreds of millions of dollars in lost production each year (Oerke et al. 2012). Among these, gardeners frequently encounter the green rose aphid (*Macrosiphum rosae* L.) on rosebushes or the black bean aphid (*Aphis fabae* Scopoli) on other garden plants (Brisson and Stern 2006). We still have almost no information on how aphids respond to urban habitats, which other species are related to gardens, and how their numbers are correlated with those of their predators. Hoverfly larvae and ladybirds are the most important predators of this group (Chapter 4, Rotheray 1989, Ball et al. 2013). Given their diversity and ubiquity, together with their range of relationships with host plants and insect predators, aphids and their enemies provide an excellent model system for examining how urbanisation affects insect abundance and diversity.

Hoverflies provide varied ecosystem services: larvae contribute to pest control feeding on aphids and other insects (insectivore species), waste decomposition (saprophagous species, eating decaying plant and animal matter), and adults are valuable pollinators of crops and other systems (Jauker et al. 2012, Moquet et al. 2017). Hoverflies have previously been shown to be negatively associated with higher levels of urbanisation (Bates et al. 2011), but how this is affected by resource availability in urban habitats is not known. Most ladybirds (Coleoptera: Coccinellidae) are main predators of aphids, coccids, mites and a variety of other arthropods, and of high interest because of their application as biological control agents (Giorgi et al. 2009, Obrycki et al. 2009, Weber and Lundgren 2009, Honek et al. 2017). Studies evaluating vulnerability of ladybird communities to urbanisation are surprisingly few. This way, investigating ladybirds numbers coupled with changes in its prey in urban environments is of great importance since it has been hypothesized that recent decreases in coccinelid numbers may be due to phenological asynchronization between host plants, insect herbivores and their coccinellid predators (Honek et al. 2017).

In this work we asked how local and fine-scale environmental factors determine the diversity of aphids and their primary predators in urban gardens. We asked this as little is known about how aphids and their predators respond to changes in urbanisation. Investigating both trophic groups at the same time (herbivores and their main predators) may provide insights as to which group may be more sensitive to urbanisation and its consequences. To address this gap in understanding, we investigated how variation in environmental factors directly (host plant abundance, garden plant richness, garden size, proportion of impervious surfaces in the surrounding area) and indirectly (prey and predator abundance) associated with urbanisation influences the local diversity and abundance of aphids, ladybirds and hoverflies.

2.2 METHODOLOGY

2.2.1 STUDY SITES AND SAMPLING

Sixty-seven domestic gardens located in Greater Reading, Berkshire, England (51°27’N, 0°58’W) were selected for this study. Greater Reading is a urban area with a population of 290 000, which covers an area of ca. 72 km^2 (Office for National Statistics 2013). These gardens were chosen from previously designated areas, which were selected by their representation of an urbanisation gradient that covers highly urbanised areas in the town centre, to periurban and suburban areas until reaching the borders of the town with agricultural areas in the south (Figure 2.1). Each target area was composed of 5-10 houses, and from each area was recruited a garden by either the distribution of leaflets or by randomly asking “door-to-door” for volunteers willing to participate in the study. While this process was not entirely random, it was considered effective in capturing local variation in garden structure as the need of gardens of all shapes, sizes and frequency of management/gardening, was emphasised in order to avoid a bias towards garden enthusiasts (Barratt et al. 2015). Each garden is located at least 240m apart.

Sampling occurred from mid-June until the beginning of August of 2017. In each study site, every plant within reach was fully searched for aphids, ladybirds and hoverfly larvae. These plants were composed mainly of ornamental plants, wild plants, potted plants, bushes, shrubs, herbs, aromatic plants, and small trees. Adult ladybirds and aphids were collected by aspiration and placed in Eppendorf tubes filled with 70% ethanol. Aphid host plants were identified. Aphid abundance was estimated using hand counters. Hoverfly and ladybird larvae were collected with paint-brushes and cotton swabs, and kept separately from the collected aphids and adult ladybirds in empty Eppendorf tubes, stored in a -20^{O}C freezer.

To determine the diversity of hoverfly adults, standardised point counts, each lasting 5 minutes and executed by 3 people, were performed in each garden, and individuals were collected for posterior identification with sweep nets. Although not all hoverfly larvae species feed on aphids (only about 40% of British species are aphid predators, Ball et al. 2013), we decided to consider all hoverfly species (both as larvae and adults) as well as only aphidophagous species in our survey and posterior analysis in order to have a comprehensive picture of the diversity of this group as whole in this study.

The insect samples were returned to the laboratory for identification to species level for hoverfly and ladybird individuals (keys used: Gilbert 1986, Majerus and Kearns 1989, Rotheray 1989, Ball et al. 2013), and aphids to morphospecies and species level (following Blackman and Eastop 1994, Blackman and Eastop 2008). Aphid identification to species level was not always possible due to the lack of mature adult aptera in samples. The ethanol and freezer stored collection are housed in the School of Biological Sciences, University of Reading, Reading, UK.

Aphid host plants were counted and identified to genus or species level. Plant species richness was estimated by visually counting plant morphospecies in each garden. Although this method is not adequate for the taxonomic censusing of plants in a particular area, it has shown to be strongly correlated to species richness and to effectively capture variance between study sites with the advantage of reduced sampling effort and effectiveness to achieve statistical power (Abadie et al. 2008, Schmiedel et al. 2016).

2.2.2 HABITAT VARIABLES

The proportion of impervious surfaces surrounding each garden was obtained using geographic information system (GIS) procedures, utilising the topography layer from the Ordnance Survey MasterMap®, at a scale of 1:1250. It is subdivided in various themes: natural environment, buildings and structures, administrative boundaries, heritage and antiquities, land, roads, gardens, rail, tracks and paths, terrain, height and water. Using QGIS 2.8.1 (QGIS Development Team 2015), 100 m radius buffers were delimited from each study site, and a reclassification of vectors was made in order to result in proportion of area made of impervious surfaces within those buffers, which comprised of buildings and structures (any building or artificial structures made of concrete, brick or stone) and roads (roads, roadsides, tracks or paths made of impervious surfaces such as asphalt). In addition, the area of each garden, comprised by both back and front garden when present, was also obtained.

We initially planned to only select gardens that are not sprayed with pesticides for this study, however, we found that the majority of garden owners that volunteered for this study utilise at least one form of insect control that might influence colonization and survival of aphids and their respective syrphid and coccinelid predators. We therefore created a classification of garden disturbance/management to utilise as an explanatory variable in our models with: 1) no, or very low intervention: no use of pesticides or use of practices that were deemed unlikely to have a great effect on insect recruitment (e.g. use of slug pellets, weed killers and other forms of insect control such as handpicking, netting); 2) mild, not recent intervention: no use of pesticides this year, but were used in the past two years; 3) high, or recent intervention: recent use of pesticides (partially, or on the majority of plants in the garden).

2.2.3 ANALYSIS

Statistical analyses were carried out using R 3.1.2 (R Development Core Team 2014). Aphid species richness was modelled through a generalised linear model (GLM) with a Poisson distribution and a log link function (Zuur et al. 2009), and aphid abundances was modelled through a GLM with negative binomial distribution and a log link function (Crawley 2007, Zuur et al. 2009) using package MASS (Ripley 2015) . As explanatory variables we used the sum of all predator abundances (abundance of ladybirds and aphidophagous hoverflies), abundance of potential host plants, garden plant richness, garden area, proportion of impervious surfaces within a 100 m radius buffer and garden disturbance/management classification (as described above).

Species richness of both hoverflies and ladybirds were not used as response variables in our models due to the lower numbers of species and low levels of variation amongst gardens. To explore which factors determine the abundance of all hoverflies and ladybirds in our study sites we performed GLMs, and as these variables were overdispersed, we used a negative binomial distribution and a log link function (Crawley 2007, Zuur et al. 2009) using package MASS (Ripley 2015). As the numbers of only aphidophagous hoverflies were quite low and none were found in many gardens, we modelled their occurrence (presence or absence) through a GLM with a binomial distribution and logit link function (Crawley 2007). As explanatory variables we used the total abundance of aphids, garden plant richness, garden area, proportion of impervious surfaces and garden disturbance. The explanatory variables of total aphid and predator abundance, garden area and host plant abundance were either squared or log-transformed in order to deal with extreme values and facilitate model fitting and convergence in all models.

Model selection was made using Akaike's Information Criteria (AIC), by fitting the full model with the set of all explanatory variables and removing the least significant term at each step, then refitting the model each time until the optimal model (with the lowest AIC) is found (Crawley 2007, Bolker et al. 2009, Zuur et al. 2009). We checked for collinearity between explanatory variables in our models through variance inflation factors (VIF), which are used as an indicator of multicollinearity in multiple regression, with VIF values higher than 3 indicating that covariation between predictors may impose a problem (Zuur et al. 2007). Our VIF values were in the range of 1.03 - 2.40. The response variables and model residuals were checked for spatial autocorrelation through spline correlograms on package ncf (Bjornstad 2015), in which we did not find any significant spatial structure.

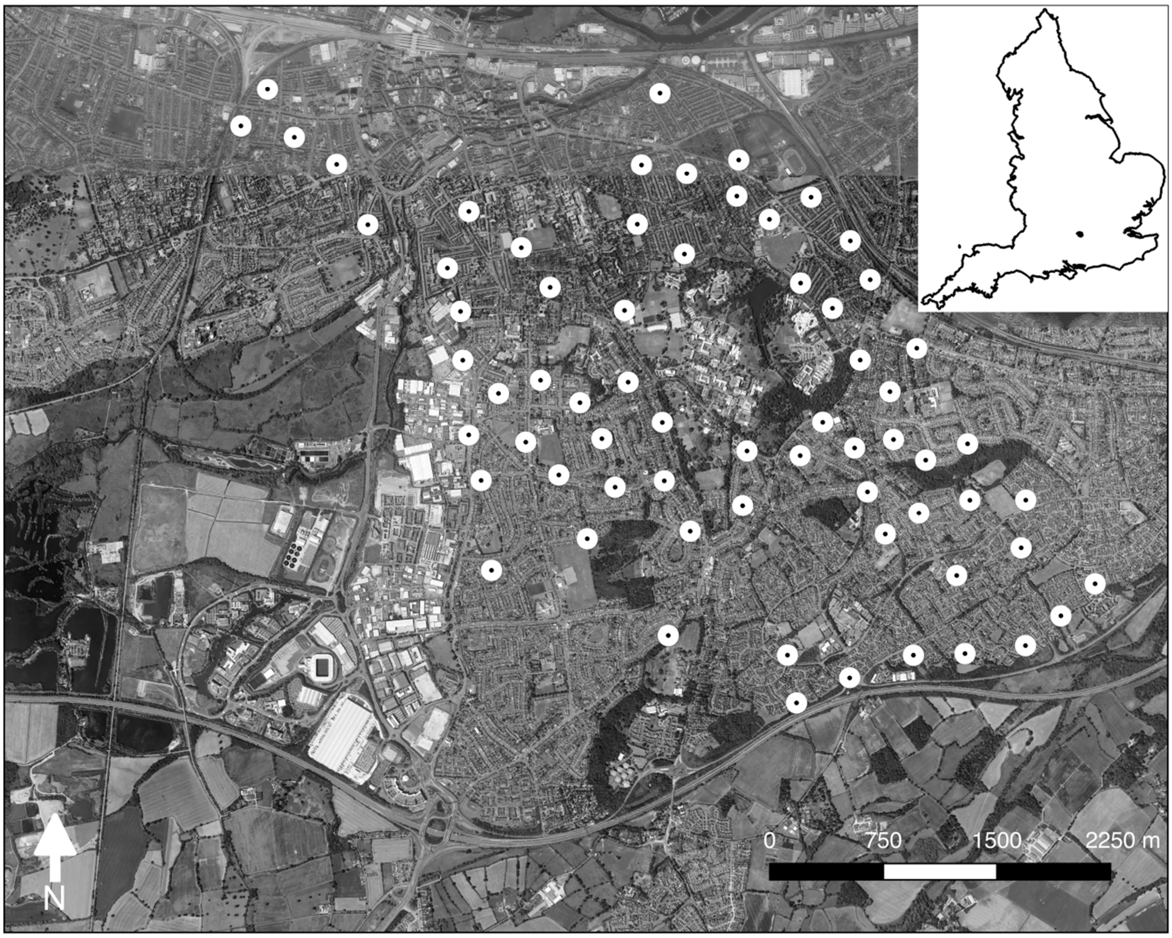


Figure 2.1. Location of sampling sites (n = 67) in Greater Reading, England. Aerial imagery was obtained from the Ordnance Survey Edina MasterMap®

2.3 RESULTS

We observed 45 aphid species (179917 individuals in total), 17 hoverfly species (494 individuals) and 9 ladybird species (173 individuals) (Table 2.1). The ants *Myrmica rubra* L. and *Lasius niger* L. were found attending aphid colonies on 87% of the study sites that had aphid colonies. The proportion of habitat elements and its maximum and minimum values are show in Table 2.2.

TABLE 2.1 Aphid, ladybird and hoverfly species recorded and their respective frequencies of occurrence.

Insecta	**Frequency of occurrence (%)**
Hemiptera	
Aphididae	
Aphis fabae Scopoli, 1763	77.61
Aphis gossypii Glover, 1877	28.36
Macrosiphum euphorbiae (Thomas, 1878)	16.42
Longicaudus trirhodus (Walker, 1849)	8.96
Uroleucon hypochoeridis (Hille Ris Lambers, 1939)	8.96
Macrosiphum rosae (Linnaeus, 1758)	7.46
Aphis craccivora Koch, 1854	5.97
Brachycaudus cardui (Linnaeus, 1758)	5.97
Brachycaudus helichrysi Kaltenbach, 1843	5.97
Sitobion fragariae (Walker, 1848)	5.97
Aphis epilobii Kaltenbach, 1843	4.48
Aphis grossulariae Kaltenbach, 1843	4.48
Aphis pomi De Geer, 1773	4.48
Aphis urticata Gmelin, 1790	4.48
Hyperomyzus lactucae (Linnaeus, 1758)	4.48
Maculolachnus submacula (Walker, 1848)	4.48
Myzus cerasi (Fabricius, 1775)	4.48
Anoecia corni (Fabricius, 1775)	2.99
Callipterinella tuberculata (von Heyden, 1837)	2.99
Aphis brohmeri Börner, 1952	1.49
Aphis epilobiaria Theobald, 1927	1.49
Aphis frangulae Kaltenbach, 1845	1.49
Aphis nasturtii Kaltenbach, 1843	1.49
Aphis parietariae Theobald, 1922	1.49
Aphis ruborum (Börner, 1932)	1.49
Aphis schneideri (Börner, 1940)	1.49

Aphis taraxacicola (Börner, 1940)	1.49
Aphis verbasci Schrank, 1801	1.49
Brachycaudus tragopogonis Kaltenbach, 1843	1.49
Chaetosiphon fragaefolii (Cockerell, 1901)	1.49
Drepanosiphum platanoidis (Schrank, 1801)	1.49
Dysaphis aucupariae (Buckton, 1879)	1.49
Macrosiphoniella millefolii (De Geer, 1773)	1.49
Macrosiphum funestum Macchiati, 1885	1.49
Myzocallis coryli (Goeze, 1778)	1.49
Myzus ornatus Laing, 1932	1.49
Myzus varians Davidson, 1912	1.49
Nasonovia ribisnigri (Mosley, 1841)	1.49
Symydobius oblongus (von Heyden, 1837)	1.49
Uroleucon picridis (Fabricius, 1775)	1.49
Wahlgreniella nervata (Gillette, 1908)	1.49
Diptera	
Syrphidae	
Episyrphus balteatus (De Geer, 1776)	46.27
Syritta pipiens (Linnaeus, 1758)	13.43
Platycheirus albimanus (Fabricius, 1781)	10.45
Melanostoma scalare (Fabricius, 1794)	8.96
Melanostoma mellinum (Linnaeus, 1758)	4.48
Eupeodes luniger (Meigen, 1822)	2.99
Sphaerophoria scripta (Linnaeus, 1758)	2.99
Epistrophe eligans (Harris, 1780)	1.49
Syrphus ribesii (Linnaeus, 1758)	1.49
Platycheirus scutatus (Meigen, 1822)	1.49
Baccha elongata (Fabricius, 1794)	1.49
Eupeodes corollae (Fabricius, 1794)	1.49
Myathropa florea (Linnaeus, 1758)	1.49
Microdon analis (Macquart, 1842)	1.49
Meliscaeva auricollis (Meigen, 1822)	1.49
Sericomyia silentis (Harris, 1776)	1.49
Eristalis tenax (Linnaeus, 1758)	1.49
Coleoptera	
Coccinellidae	
Harmonia axyridis (Pallas, 1773)	32.84
Propylea quatuordecimpunctata (Linnaeus, 1758)	20.90
Coccinella septempunctata (Linnaeus, 1758)	7.46
Psyllobora vigintiduopunctata (Linnaeus, 1758)	2.99
Halyzia sedecimguttata (Linnaeus, 1758)	2.99
Harmonia quadripunctata (Pontoppidan, 1763)	1.49
Adalia decempunctata (Linnaeus, 1758)	1.49
Exochomus quadripustulatus (Linnaeus, 1758)	1.49
Chilocorus renipustulatus (Scriba, 1791)	1.49

TABLE 2.2 Mean proportion (± SE) and range of habitat elements within 100 m buffers of the study sites.

	Host plant abundance	Plant richness	Garden area	Impervious surfaces
Mean (±SE)	30.33 ± 5.44	49.75 ± 4.84	340.96 ± 37.21	0.39 ± 0.01
Range	0 - 269	4 - 172	28.91 - 1653.56	0.17 - 0.71

2.3.1 BIOTIC AND ABIOTIC FACTORS DETERMINING APHID, LADYBIRDS AND HOVERFLY NUMBERS IN URBAN GARDENS

The best model in explaining the species richness of aphids in our study sites had two positive and significant explanatory factors, the abundance of host plants and plant species richness within each garden (Table 2.3, model 1, Figure 2.2), garden area, predator abundances, and garden disturbance/management were removed due to non-significance and low explanatory power during the model selection process. The most parsimonious model in explaining aphid numbers had only one variable, which was abundance of host plants (Table 2.3, model 2, Figure 2.3), and other explanatory variables listed in the analysis section were removed during the model selection process. The best model for explaining the total abundance of hoverflies had only one positive explanatory variable, which was garden plant richness (Table 2.3, model 3, Figure 2.4). Other explanatory variables (garden area, aphid abundances, and garden disturbance/management) were removed during the model selection process when related to this variable. The best final model that explains occurrence of aphidophagous hoverflies have two explanatory variables, garden plant richness, which was positively and significantly related to aphidophagous hoverfly presence, and garden disturbance/management, with low levels of garden management positively related to the presence of aphidophagous hoverflies, however this factor was not statistically significant (Table 2.3, model 4, Figure 2.5). Lastly, the best model in describing variance in ladybird abundance had three variables: aphid abundance and plant species richness, which were positively and significantly correlated with ladybird abundance, and the proportion of impervious surfaces in a 100 m radius buffer, which was negatively correlated with the abundance of ladybirds (Table 2.3, model 5, Figure 2.6). Garden area and garden management levels were removed during the model simplification process due to low explanatory power when predicting this variable.

TABLE 2.3. Summary of best models predicting aphid species richness (model 1 and 2), and abundance and occurrence of hoverflies (model 3 and 4) and ladybirds (model 5) in urban gardens across Reading, UK. AIC values for each model are given, and significant explanatory factors are shown in bold.

Model ID	AIC	Response variable	Explanatory variable	Coefficient value ± SE	P
1	241.76	Aphid richness	Intercept	-0.084 ± 0.192	0.662
			Host plant abundance	0.772 ± 0.125	7.13E-10
			Plant richness	0.005 ± 0.002	0.01
2	1137.2	Aphid abundance	Intercept	5.917 ± 0.364	2.00E-16
			Host plant abundance	1.504 ± 0.284	1.16E-07
3	397.46	Hoverfly general	Intercept	1.156 ± 0.195	3.24E-09
			Plant richness	0.014 ± 0.003	2.76E-06
4	78.193	Hoverfly aphidophagous	Intercept	-3.915 ± 1.578	1.30E-02
			Plant richness	0.049 ± 0.014	7.88E-04

			Low intervention	2.334 ± 1.244	0.061
5	237.26	Ladybird	Intercept	-2.017 ± 0.952	0.034
			Aphid abundance	0.873 ± 0.222	8.36E-05
			Plant richness	0.018 ± 0.005	6.72E-05
			Impervious surfaces	-3.016 ± 1.53	0.049

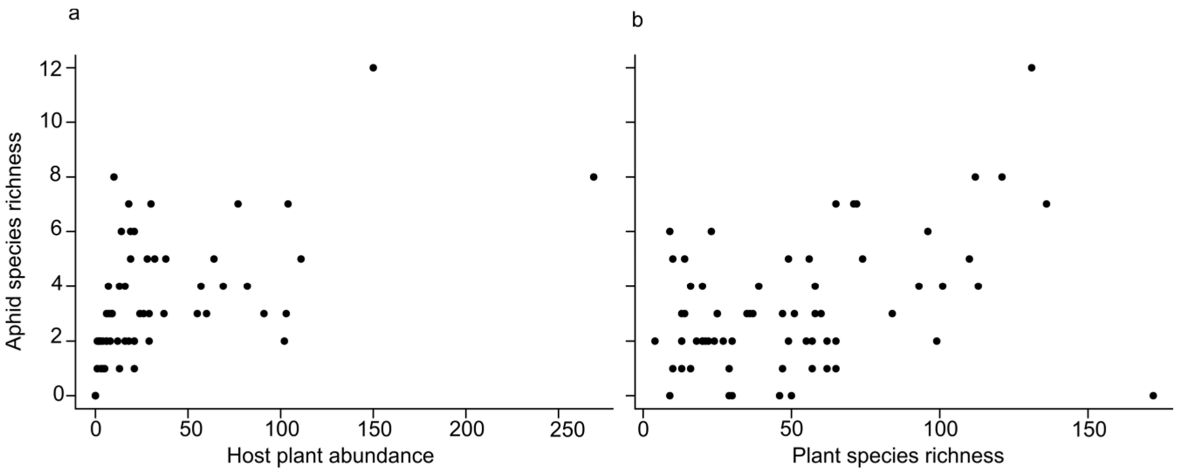


FIGURE 2.2. Aphid species richness according to (a) host plant abundance and (b) plant species richness in urban gardens across Reading, UK.

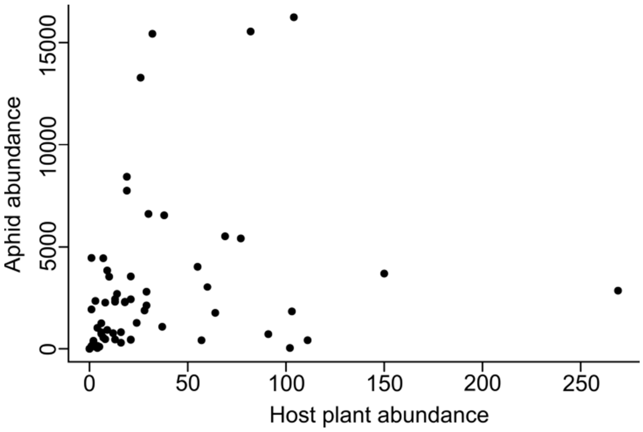


FIGURE 2.3. Aphid abundances according to host plant abundance present in gardens across Reading, UK.

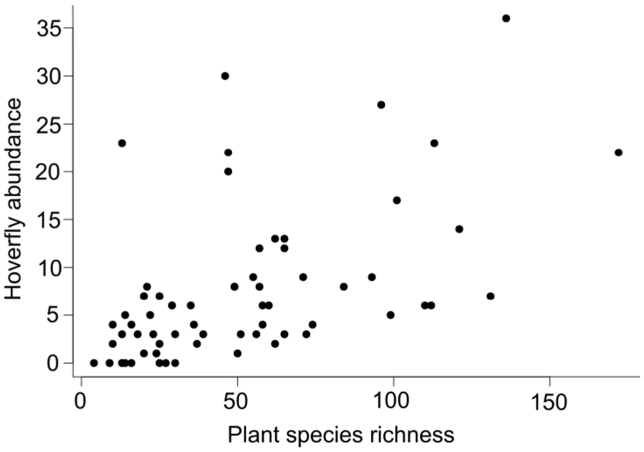


FIGURE 2.4. Hoverfly abundance in relation to plant species richness in urban gardens across Reading, UK.

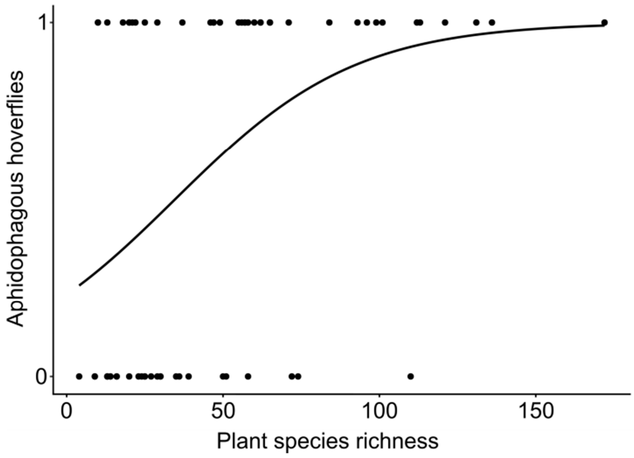


FIGURE 2.5. Representation of logistic regression model of plant species richness present in urban gardens determining the presence (1) or absence (0) of aphidophagous hoverflies.

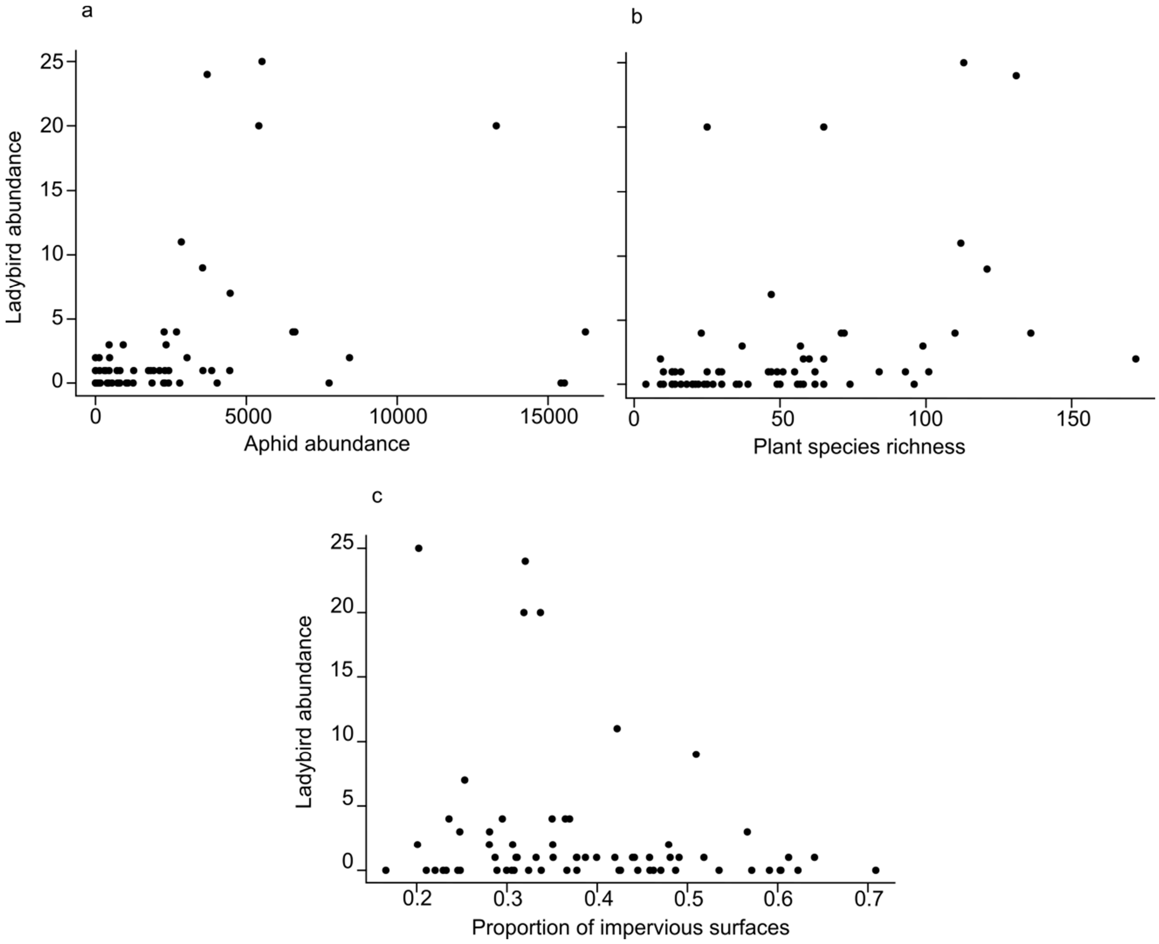


FIGURE 2.6. Ladybird abundance in relation to (a) aphid abundance, (b) plant species richness and (c) proportion of impervious surfaces in urban gardens across Reading, UK.

2.4 DISCUSSION

In this study, we found that aphid species richness and abundance were positively associated with host plant abundance and garden plant species richness, both traits of gardens largely determined by the homeowner. Hoverfly numbers, including all specimens and aphidophagous species alone, were only positively and significantly correlated with garden plant richness, although aphidophagous individuals also appear to be positively associated to low pesticide use and garden disturbance. However, this factor was not statistically significant. The abundance of ladybirds was significantly and positively correlated to aphid abundance and garden plant species richness, and negatively associated to the proportion of impervious surfaces. This contrast between the two major taxa of aphid predators may reflect differences in behaviour. While the larvae of both groups are aphidophagous, as are adult ladybirds, adult hoverflies feed upon pollen and nectar.

As sessile and specialised phytophagous groups, aphids are undoubtedly intrinsically linked to plant diversity and structure, and are known to be affected by plant diversity manipulation in grasslands (Koricheva et al. 2000). Many species of aphids exhibit host alternation, where different generations live on two taxonomically unrelated host plants (Rotheray 1989). Aphids can therefore be considered “sequential polyphages” (Andow 1991) and may reach higher densities on areas that contain several plant functional groups because such places are more likely to contain both the primary and the secondary host plants (Koricheva et al. 2000). Therefore, the positive association of aphid species richness and abundances with garden plant richness and host plant numbers found in our study was not surprising.

Urban gardens are areas of exceptionally high levels of plant diversity. In comparison to other habitats, gardens present higher plant species richness (1056 species in 267 gardens of five UK cities) (Gaston et al. 2007, Goddard et al. 2010). Nevertheless, this artificially high level of plant diversity results from gardening practices that support and select exotic species, which can sometimes can reach elevated densities (Goddard et al. 2010). According to Gaston et al. (2007), about 70% of the UK garden flora is exotic. Little is known and discussed about the contribution of the ornamental exotic plant trade to aphid invasion (Kiritani and Yamamura 2003), but certainly the spread of the range of host-plants available, both locally and regionally, may contribute to increases of new host-plant relationships with native fauna, as well as facilitate the establishment and spread of exotic species (Honek et al. 2017). In our samples, we found four non-native species of aphid (*Macrosiphum euphorbiae*, *Aphis gossypii, Myzus varians* and *Wahlgreniella nervata*).

In our work, we found no evidence of an association between increased urbanisation and aphid diversity. There are very few studies investigating this subject. Andrade et al. (2017), while investigating how urbanisation affects aphids in an arid city using an 11 year dataset, found no relationship between aphid numbers and urbanisation level. Instead, aphid abundance varied along a gradient of water availability and vegetation density. The authors argued that aphids are able to thrive in urban areas based on their ability to exploit an increase in resource availability in urban and disturbed habitats, despite fragmentation within the surrounding matrix, and proposed that the group should be regarded as urbanophiles.

In our study, hoverflies responded significantly to garden plant richness as an explanatory factor. This was not surprising given that adults feed on the pollen and nectar of flowering plants (Haenke et al. 2009, Moquet et al. 2017). Foraging theory proposes that hoverflies would prefer to visit sites with high floral density because such sites might provide higher amounts of resources at a low foraging cost (Meyer et al. 2009, Moquet et al. 2017). Consequently, it is expected that hoverflies will be positively related to flowering rich habitats like gardens and flowering rich field margins (Cowgill et al. 1993, Hickman and Wratten 1996, Haenke et al. 2009). Blackmore and Goulson (2014) compared urban plots, which were previously sown with wildflowers in amenity grasslands, with unaugmented controls, and showed that sown plots had 25 times more flowers and 13 times more hoverflies compared to the paired control plots. Such simple interventions have already proved to be effective in enhancing hoverflies and bumblebees in agricultural areas (Pywell et al. 2011).

Baldock et al. (2015), when comparing between three different landscapes/habitats, found that the abundance of hoverflies was higher in farmland and nature reserves than in urban sites. Syrphid flies did not respond to our measure of urbanisation, which was the amount of impervious surfaces in 100 m radius buffers. In a previous study carried out by Haenke et al. (2009) in agricultural landscapes, showed that syrphid flies responded best on environmental factors measured on scales between 0.5-1 km. Hoverflies are highly mobile organisms with excellent vision which are able to easily detect areas containing resources within matrixes of non-nutritious environments (Bernard and Stavenga 1979, Lunau and Wacht 1994, Haenke et al. 2009). That could mean that the scale utilised by our work might not be biologically meaningful for this taxon. However, similar studies have reported that the abundance of hoverflies is correlated to local and fine-scale environmental variables, e.g. being more abundant in gardens containing ponds (Smith et al. 2006a).

Although we expected that aphidophagous hoverflies would be positively correlated with the total abundance of aphids in a garden, this factor was not significant, and that might be due to the small number of aphidophagous species collected. Hoverfly adults rely on floral resources for feeding, and this contrasts to coccinelids which both adults and larvae rely in a more strictly aphidophagous diet (Rotheray 1989). Syrphids as a group can be found on a variety of different microhabitats, larvae might breed and feed in places such as tree holes, decaying matter, ponds, drainage ditches or vegetation (Hennig and Ghazoul 2012), and also present an overall varied diet (phytophagous, saprophagous and zoophagous) (Moquet et al. 2017). This way, syrphid flies are probably associated to the availability of these varied larval resources and specific microhabitats (Haenke et al. 2009), which were not assessed by this study.

A characteristic typical of predatory ladybirds is the aggregation of many individuals on plants that contain abundant supplies of prey, consequently, the composition of these communities is determined by prey identity, their numbers, microclimate and plant composition (Ferrer et al. 2016, Honek et al. 2017). Our results corroborate these characteristics, since ladybirds numbers correlated positively with total numbers of aphids in gardens as well as garden plant richness. The flora of cities often harbours great numbers of coccinellids (Gardiner et al. 2014). However, by providing a suitable microclimate and an abundance of prey, vegetation in urban green spaces can also host invasive species (Honek et al. 2017), such as *Harmonia axydiris*, a widespread coccinellid invader from Asia, frequently found on our samples.

Ladybird abundance was also negatively associated with the proportion of impervious surfaces surrounding each garden, and the construction of buildings and replacement of native by exotic vegetation have been previously suggested as possible barriers to coccinellid movement (Honek et al. 2017). Urban land cover can increase the likelihood of local extinction and reduce the likelihood of colonisation for ladybird beetles in the UK (Comont et al. 2014). Therefore, while gardens and parks in urban areas often seem to be favourable for some species of ladybird, our results indicate that overall increases in urban land cover are not favourable for ladybirds as a group, a conclusion also drawn by Comont et al. (2014), who suggest that urban areas are probably beneficial for a small subset of habitat generalist species but poor for more specialist species (see Chapter 4). This may be the result of destruction and fragmentation of the preferred habitats of specialist species, which can promote biotic homogenisation (McKinney 2006), but may also be exacerbated by competition from increased numbers of generalists and invasive species such as *H. axyridis* in urban areas (Comont et al. 2014).

Natural enemies are vital for the management and function of greenspaces, since they are crucial agents of biocontrol services (Burkman and Gardiner 2014), and our results shows that fragmentation and general reductions in greenspace might represent threats to biodiversity and consequently the ecosystem services it provides. Green spaces in towns and cities can help reduce the extent of the impact caused by urbanisation, since it provides resources and shelter as well as serving as corridors between non-suitable habitats in the urban matrix (Smith et al. 2006a). Urban gardens associated to residential areas are demonstrating to be one of the most important portions of urban green spaces, which show to contain a great parcel of the biodiversity present in a region, at least in the UK (Owen 1991, Gaston et al. 2005, Loram et al. 2007). Even though conservation practices are concentrated in urban reserves and parks, private gardens have been showing to present a valuable part of urban biodiversity (Smith et al. 2006a, Goddard et al. 2010). Another often unrecognized aspect of urban domestic gardens is that many people will have their closest contact with wildlife and biodiversity through it, hence gardens might enable people to perceive and appreciate nature (Cannon 1999, Smith et al. 2006a). Fundamentally, our current understanding of how species, and in particular widespread and common invertebrates, respond to urbanisation is limited to a small number of well-studied taxa. Our work shows that, for our study system, the planting decisions made by garden owners have great positive influence on the diversity and abundance of aphids and their enemies. We suggest that such benefits are likely to be felt throughout urban ecosystems, where the aesthetically-motivated decisions of gardeners have much wider positive benefits for biodiversity. The present work focused on patterns of diversity of important groups of invertebrates found in urban gardens, however there is still much to be learnt about general and specific factors determining the diversity of many other taxa, as well as appropriate garden management actions that could benefit overall biodiversity in such habitats.

Chapter 3 INTERACTIONS BETWEEN HERBIVORES, NATURAL ENEMIES AND MUTUALISTS ARE INFLUENCED BY URBANISATION

3.1 INTRODUCTION

Urbanisation is the defining feature of recent history; today over 50% (>90% in developed countries) of people live in urban environments (United Nations 2014). Urbanisation is arguably the greatest anthropogenic transformation that ecological systems experience and questions of how urban ecosystems may differ from more natural systems is a question that has very recently moved to the forefront of global concerns (Grimm et al. 2008, Kowarik 2011, Pickett et al. 2011).

While most studies of urban ecology examine changes to the diversity and abundance of species present in towns and cities, attention has only started to focus on how assemblages of interacting species are formed in urban areas, and how this is affected by the intensity of urbanisation (Bennett and Gratton 2012, Quispe and Fenoglio 2015, Pereira-Peixoto et al. 2016, Turrini et al. 2016). Fragmentation reduces populations of native plants (Benitez-Malvido 1998, Jules 1998, Williams et al. 2005), while urban soils tend to be more alkaline (from concrete and other lime-based materials), favouring plants with high-pH soil requirements (Gilbert 1989) and a wide range of ornamental plants are introduced (Smith et al. 2015).

Fragmentation leads to decreased connectivity between patches containing vegetation and existing patches tend to be smaller (Medley et al. 1995, McKinney 2002), and therefore of reduced habitat quality for many animal species (Bradley and Altizer

2007, Bang and Faeth 2011, Faeth et al. 2011, Turrini et al. 2016). There are also some dramatic physical changes that arise from increased densities of sealed and impermeable areas, such as buildings and roads, and also microclimatic alterations like the urban heat island effect (Bradley and Altizer 2007, Bang and Faeth 2011, Faeth et al. 2011), which produces locally higher temperatures in comparison to the surrounding landscape (Lo et al. 1997, Collins et al. 2000). Together, these changes affect the likelihood of encountering species at higher trophic levels (Faeth et al. 2005). Understanding how such extreme anthropogenic habitat changes may affect patterns of ecological interactions is perhaps most tractable with arthropod model systems (McIntyre 2000, Bang and Faeth 2011), but experimental studies in urban ecosystems are few.

Urbanisation has been shown to affect the structure of insect communities, resulting in dramatic changes in their abundance and richness (McIntyre 2000, Grimm et al. 2008, Raupp et al. 2010), most frequently leading to a loss of diversity (Kahn and Cornell 1989, Suarez et al. 1998, McKinney 2002, Shochat et al. 2004b, Rango 2005, Pauchard et al. 2006, Sadler et al. 2006, Clark et al. 2007, Magura et al. 2010, Uno et al. 2010, Bang and Faeth 2011, Bennett and Gratton 2012, Ramírez Restrepo and Halffter 2013). Rarely studies have considered how these changes influences the outcome of ecological interactions at multiple trophic levels (Bennett and Gratton 2012, Fenoglio et al. 2013, Pereira-Peixoto et al. 2016, Turrini et al. 2016). Abiotic environmental factors interfere and modulate biotic interactions, having indirect consequences on food webs (Ritchie 2000, Preisser and Strong 2004, Turrini et al. 2016). If, as expected, insects and other arthropods do respond to habitat structure, then we can predict that there will be differences not only on species assemblages, but also on trophic dynamics and species interactions as habitat configuration changes with urbanisation.

As an example, in urban areas where the structure of vegetation is simplified in comparison with the non-urban matrix, it can present reductions in diversity of natural enemies and environmental services they provide, such as pest regulation (Hanks and Denno 1993, Shrewsbury and Raupp 2006, Raupp et al. 2010). As a consequence of species differentially responding to alterations in their environment, human-induced changes affect trophic levels in distinctive ways (Harrington et al. 1999, van der Putten et al. 2004).

If we consider that urban-dwelling organisms are subject to multiple changes in abiotic conditions simultaneously, it is not surprising that predicting the consequences of such changes for trophic processes and for direct and indirect species interactions is highly challenging (Turrini et al. 2016). However, a few trends have begun to appear. Urban areas are often characterized by reduced numbers of native vertebrate predators (McKinney 2002, Shochat 2004), an increased abundance of some urban adapted species, which can potentially lead to increased competition and displacement (Hostetler and McIntyre 2001), altered behaviour and phenology (Connor et al. 2002, Neil and Wu 2006), high densities of herbivorous arthropods (Dreistadt et al. 1990, Hanks and Denno 1993, Watson et al. 1994, Tooker and Hanks 2000), lower numbers of arthropod predators (Rango 2005, Turrini et al. 2016), lower numbers of parasitoids (Denys and Schmidt 1998, Bennett and Gratton 2012). All these changes can potentially lead to altered trophic structure, and we must recognize that trophic dynamics cannot be understood based only on our knowledge of species composition (Shochat et al. 2006). This way, evaluating empirically how trophic dynamics behave in urban environments might help us to make some broad and useful predictions regarding the effects that urbanisation could have on multi- trophic interactions.

On direct trophic interactions such as predation one species has a negative effect on the other species, but in indirect interactions one species can also positively affect another species through intermediate levels in a food web (Halaj and Wise 2001, Turrini et al. 2016). For example, the presence of some species of honeydew-collecting ants results in increased numbers of aphid parasitoids when protecting aphids from predators, and incidentally also protecting parasitized aphids against predators and hyperparasitoids (Völkl 1992, Kaneko 2002). Nevertheless, the most recognized indirect trophic interactions is the top-down control in which predators influence plants by feeding on herbivores, thus reducing the consequences of herbivory (Schmitz et al. 2000, Shurin et al. 2002, Turrini et al. 2016). However previous studies have shown that this type of interaction might be altered in urban habitats (Webb and Hopkins 1984, Kruess and Tscharntke 1994, Pereira-Peixoto et al. 2016, Turrini et al. 2016).

Host-parasitoid interactions are also likely to be considerably altered in urban ecosystems. Here, plant resources for herbivorous insects and their parasitoids are spatially divided in a matrix of built environment (Kotze et al. 2011, Bennett and Gratton 2012, Fenoglio et al. 2013). These conditions are particularly prone to affect insect colonization and persistence, which may lead to altered trophic interactions (Fenoglio et al. 2013). Parasitoid insects are important biological control agents of herbivorous insect populations and have been found to be negatively affected by urbanisation at different spatial scales (Bennett and Gratton 2012, Fenoglio et al. 2013). Parasitoids are specialists organisms closely associated to their hosts (Kruess and Tscharntke 1994). Consequently, they might present higher sensitivity to environmental fluctuations and anthropogenic disturbances in comparison to other less specialized species (Gibb and Hochuli 2002). Since some herbivore pest populations are often limited by top-down control of parasitoids (Hawkins and Gross 1992), a decrease in parasitism or predation control can favour pest outbreaks (Schmitz et al. 2000, Roslin et al. 2014), and affect ecosystem functioning and stability (van der Putten et al. 2004, Faeth et al. 2005).

Traditionally, research on trophic interactions and food webs mainly focus on direct interactions such as predation or parasitim, therefore the importance of non-trophic, indirect, and facilitative interactions has been rarely taken into consideration (Ohgushi 2008). Facilitative or positive interactions, like mutualisms, are rarely considered as potential factors affecting urban populations and communities (but see e.g. Thompson and McLachlan 2007, Gibb and Johansson 2010, Toby Kiers et al. 2010), and it is claimed that this type of positive interaction play an important part in the structuring of some biological communities by providing refuge from predation or competition (Stachowicz 2001). Conversely, is important to notice that mutualisms have formed and dissolved over evolutionary time scales, and we still do not know if mutualisms have evolved to be resilient enough to endure anthropogenic disturbances (Sachs and Simms 2006, Toby Kiers et al. 2010).

Even less frequently considered is how these different ecological interactions (host–parasitoid, predator-prey, mutualisms) act together to affect the insect assemblages found in urban environments. Systems including different types of interactions and trophic groups have only recently started to be empirically examined

(Halaj and Wise 2001, Lurgi et al. 2016). In order to increase our knowledge about the effects of urbanisation on ecosystem functioning, a mechanistic understanding of species interactions in cities is needed (Turrini et al. 2016).

In this work we examine these interrelated biological interactions in an urban environment. We use a study system which consisted of experimental colonies of the herbivorous aphid *Aphis fabae* Scopoli reared on an herbaceous plant species (the dwarf broad bean *Vicia faba* L.) and their naturally occurring predators, parasitoid wasps and mutualistic ants along an urbanisation gradient in a large town in southern England. Study sites varied in the amount of impervious surfaces, green areas and plant species richness present. Here, we ask a) if the relative performance of aphid colonies was associated with urbanisation; b) if the presence of natural enemies (insect predators, parasitoids) and mutualists (ants) found on colonies was determined by urbanisation or aphid numbers and c) how both biotic factors (the assemblage of natural enemies and mutualists; green areas; plant species diversity and aphid numbers) and abiotic factors (impervious surfaces; distance from urban centre) act in concert to affect herbivore population sizes and the occurrence of mutualists and natural enemies.

3.2 METHODS

3.2.1 STUDY SITES AND HABITAT VARIABLES

Study sites were located in Greater Reading, Berkshire (51°27’N, 0°58’W), a large town in southern England with a population of 290 000, which covers an area of ca. 72km^2 (Office for National Statistics 2013). Twenty seven experimental sites were selected, and the selection was made in order to capture an approximate gradient from very urbanised environments in the town centre to suburban areas located on the south, covering areas of carparks, churchyards, vacant lots, parks, private and community gardens and woodlands. Each study site was at least 110 meters apart.

Land-use data for habitat categories were derived from the Ordnance Survey MasterMap® Topography layer, which represents topography at a scale of 1:1250. It is subdivided in land and vegetation types, buildings and structures, roads and paths, rails, water, terrain, height, and heritage. Using GIS techniques 30 meter radius buffers were delimited from the sites where the experimental plants were located, and then a reclassification of the themes was performed to result in proportions of area of the following habitat types within those buffers: green areas, which was composed of gardens and lawns with ornamental plants, bushes, trees, and shrubs; impervious surfaces, which was composed of buildings (any building or artificial structures made of concrete, brick or stone) and byways (roads, roadsides, tracks or paths made of impervious surfaces such as asphalt). This procedure was carried using QGIS 2.8.1 (QGIS Development Team 2015). In addition to these habitat variables, plant species richness within a 30m radius of the study sites was estimated during the experimental period by the counting of plant morphospecies, and distance to the urban centre (m), calculated from each study site to a predetermined point in the town. This variable was used as proxy for urbanisation as cities and towns frequently show gradients of urbanisation from their centers to their edges (Deichsel 2006, Clark et al. 2007, Bang and Faeth 2011).

3.2.2 STUDY SYSTEM AND SUMMER RECORDING

The black bean aphid *Aphis fabae* Scopoli were maintained in a monoclonal culture in the laboratory using plastic and mesh cages. Cultures were kept at a constant temperature of 20 ± 1 °C and 16:8h L:D light regime at ambient humidity on broad bean, *Vicia faba* L. (var. the Sutton dwarf). Three days before being allocated to the study sites, three adults were transferred from the culture and reared on 14-16 day old dwarf broad bean plants (18-22 cm in height), to allow new colonies to become established. These plants were sown in pots with traditional potting compost (Vitax Grower, Leicester, England), and watered as required. After three days, the established aphid colonies on broad bean plants were transferred to the 27 study sites.

Two days after experimental colonies were placed in the field, species and numbers of aphids, predators, ants and parasitized aphids (mummies) were recorded, and then subsequently every four days for five recording days. At the end of this sampling period the plant/aphid-colonies were removed and replaced by new ones in the field. Sampling was repeated four times in 2015 (sampling period one: May 16th, 20th, 24th, 28th and June 1st; period two: June 15th, 19th, 23th, 27th and July 1st; period 3: 16th, 20th, 24th, 28th of July and August 1st; period four: August 14th, 18th, 22th, 26th and 30th).

3.2.3 DATA ANALYSIS

All statistical analyses were carried out using R 3.1.2 (R Development Core Team 2014). The dataset used to analyse aphid numbers consisted of the cumulative numbers of predators, ants, aphids and aphid mummies of the five counting events on each of the four sampling periods. Some colonies were lost during the four sampling periods (three colonies on the first sampling period, eight colonies on the second sampling period, three colonies on the third sampling period and four colonies on the fourth sampling period), caused by poor plant health or herbivory of plants by snails and slugs and also damage or theft by the public. This resulted in 94 observations for analysis.

All counts of aphids, predators, ants, mummies and plant richness were either log-transformed or squared root-transformed to deal with extreme values and to standardize and homogenize residuals (Crawley 2007, Zuur et al. 2009). To analyse aphid colony numbers we used a linear mixed model fitted by reduced maximum likelihood using package nlme (Pinheiro et al. 2016), and as fixed factors (explanatory variables) we used proportion of impervious surfaces, plant richness, distance to the town centre, predator abundance, number of ants farming the colony, parasitized mummies and an interaction factor between ants and predator numbers. We accounted for repeated sampling of the colonies through time by adding period as a random effect. We removed the variable proportion of green areas from the set of explanatory variables since it was highly correlated to proportion of impervious surfaces (-0.92).

To deal with the excess of zeros when modelling both ants, predators and parasitized mummies as response variables we transformed these variables as factors (presence or absence) and ran generalized logistic regressions models with a binomial error distribution family (with canonical link logit) using the function glmer of package lme4 (Bates et al. 2015), with period as a random effect and fitted by maximum likelihood (Crawley 2007). When modelling predators we used the proportion of impervious surfaces, plant richness, distance to the town centre, aphid abundance, number of ants farming the colony, and number of parasitized mummies as explanatory factors. When modelling ants as response variable we used the proportion of impervious surfaces, plant richness, distance to the town centre, predator abundance, aphid numbers, and numbers of parasitized mummies. When analysing parasitized mummies as response variable we removed the first sampling period from the dataset since no mummies were found on this period (leaving 69 observations in total), then we modelled this as a function of the proportion of impervious surfaces, plant richness, distance to the town centre, predator abundance, aphid numbers, and number of ants.

Model selection was made by comparing all candidate models using Akaike's Information Criteria (Burnham and Anderson 2003), by developing a series of alternative mixed effect models that include different combinations of the explanatory variables (Zuur et al. 2009), by fitting the full model with the set of all possible explanatory variables and taking out the least significant term on each step (Crawley 2007). We then ranked the models according to AIC Differences ($\Delta_i = AIC_i - AIC_{min}$, where AIC_i is the model i value, and AIC_{min} is the best model value). Models with $\Delta_i < 2$ provide substantial support for a candidate model, while values of Δ_i between 4 and 7 provide less support, and $\Delta_i > 10$ indicates that the model is unlikely. We also calculated Akaike weights for all models, where these model weights can be used to indicate the overall importance of a model, and higher weights indicate the chance of a model as the overall best model (Anderson et al. 2000). Aikaike weights can also be used to calculate the relative importance of a explanatory variable by summing the Akaike weights of all models that include that variable (Burnham and Anderson 2003).

We checked if collinearity could be a potential issue in our models through variance inflation factors (VIF) which is used as an indicator of multicollinearity in multiple regression, with VIF values higher than 3 indicating that covariation between predictors may be a problem (Zuur et al. 2007). All our VIF values were in the range of 1.34-2.94. All response variables were checked for spatial autocorrelation through spline correlograms on package ncf (Bjornstad 2015), and we did not find any significant spatial structure in the response variables. We assessed the validity of all models by checking normality, independence and homogeneity of model residuals.

3.3 RESULTS

In total we observed 30557 aphids, 146 predators, 660 ants and 448 mummies on our experimental plants. The ants attending the aphid colonies were *Myrmica rubra* (L.) and *Lasius niger* (L.). The predators were composed mainly by spiders (Arachnida; 59%) and hoverfly larvae (Diptera: Syrphidae; 21%), aphid midges (Cecidomyiidae; 7%), flower bugs (Hemiptera: Anthocoridae; 6%), ladybirds (Coleoptera: Coccinellidae; 3%) and in smaller amounts (4%) of earwigs (Dermaptera: Forficulidae), harvestmen (Arachnida) and lacewings (Neuroptera). The proportion of habitat elements and its maximum and minimum values in the study sites are show in Table 3.1.

TABLE 3.1. Mean proportion and number (±SE), maximum and minimum values of habitat elements within 30 meter buffers of the study sites.

	Plant richness	Impervious surfaces	Green areas
Mean (±SE)	35.86 ± 3.42	0.425 ± 0.051	0.526 ± 0.050
Max	100	0.862	1
Min	14	0	0.138

3.3.1 APHID ABUNDANCE

Model selection based on AIC differences revealed three model candidates (Δ_i <2) for explaining variance on aphid numbers, the first with predators, ants, and parasitoids; the second with predators and ants and the third only with numbers of ants farming aphid colonies (Table 3.2, models 1,2,3). However, Akaike weights indicated that the first and third models are more likely to be the best models for explaining aphid numbers (Table 3.3), with ants farming the aphid colony with the highest variable importance, being positively correlated with aphid's increase (0.885- based on the sum of Akaike weights within models with Δ_i <2) (Figure 3.1).

TABLE 3.2. Summary of model selection statistics for models predicting aphid abundance, and presence/absence of predators, ants faming the aphid colonies and parasitized mummies. Only models with substantial support (δ_i<2) are shown, and models highlighted in bold are considered the best model candidates and are further described on table 3. Δ_i= AIC differences, calculated by subtracting the model with lowest AIC value from other model AIC values. W= Akaike weights, higher weights indicate increased model importance. ImpSurf = proportion of impervious surfaces within 30m buffers; Plantrich = plant species richness within 30m; DistCentre = distance to each study site to the town centre**.**

Model ID	Response variable	Explanatory variables/Model	AIC	Δ_i	W
1	**Aphids**	**Predators+Ants+Parasitoid**	**141.02**	**0**	**0.347**
2	Aphids	Predators+Ants	141.67	0.65	0.251
3	**Aphids**	**Ants**	**141.4**	**0.38**	**0.287**
4	Predators	ImpSurf+PlantRich+Aphids+Ants	118.67	1.133	0.265
5	**Predators**	**ImpSurf+Aphids+Ants**	**117.53**	**0**	**0.467**
6	Ants farming	PlantRich+Aphids+Predators+Parasitoid	105.55	1.395	0.216
7	**Ants farming**	**Aphids+Predators+Parasitoid**	**104.16**	**0**	**0.434**
8	Ants farming	Aphids+Predators	105.83	1.673	0.188
9	**Parasitoid**	**DistCentre+Aphids+Ants**	**57.67**	**0.45**	**0.315**
10	**Parasitoid**	**Aphids+Ants**	**57.22**	**0**	**0.395**

TABLE 3.3. Summary of the best candidate models predicting aphid numbers, and presence/absence of predators, ants faming aphid colonies and parasitized mummies. Significance and coefficient values for each explanatory factor are given.

Model ID	Response variable	Explanatory variable	Coefficient value ± SE	P
1	Aphids	Intercept	1.860 ± 0.276	0
		Predators	0.135 ± 0.057	0.021
		Ants farming	0.232 ± 0.092	0.014
		Parasitoids	0.271 ± 0.119	0.026
3	Aphids	Intercept	2.024 ± 0.290	0
		Ants farming	0.280 ± 0.083	0.001
5	Predators	Intercept	-0.489 ± 0.791	0.536
		Impervious surfaces	-2.179 ± 1.004	0.030
		Aphids	1.103 ± 0.375	0.003
		Ants farming	-1.040 ± 0.458	0.023
7	Ants farming	Intercept	-3.256 ± 1.047	0.002
		Aphids	1.340 ± 0.469	0.004
		Predators	-0.759 ± 0.321	0.018
		Parasitoids	1.108 ± 0.632	0.08
9	Parasitoids	Intercept	-5.829 ± 1.861	0.002
		Distance to town centre	-0.000 ± 0.000	0.226
		Aphids	2.330 ± 0.828	0.005
		Ants farming	1.215 ± 0.625	0.052
10	Parasitoids	Intercept	-6.289 ± 1.771	0.000
		Aphids	2.121 ± 0.759	0.005
		Ants farming	1.298 ± 0.622	0.037

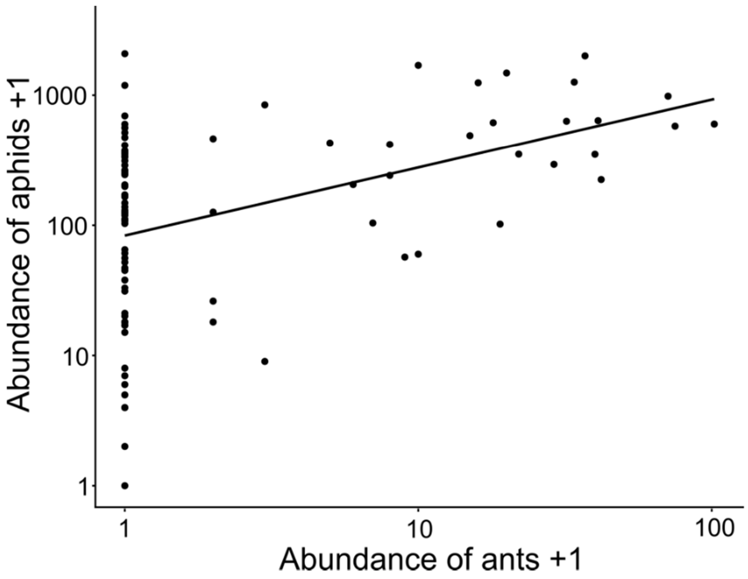


FIGURE 3.1. Relationship between abundance of aphids and numbers of ants farming the aphid colonies throughout the four sampling periods. Although linear mixed-effects models were performed (see methods), the linear model trend line is shown to illustrate the relationship between variables. Note log scale used on y and x axis.

3.3.2 APHID PREDATORS

Based on AIC differences two models were selected as model candidates for explaining the presence of predators on aphid colonies (Table 3.2, models 4 and 5), however since model 5 is 1.76 times more likely to be the best model (evidence ratio = 0.467/0.265) we choose this model as the overall best model. As explanatory factors this model included proportion of impervious surfaces, which negatively determined predator presence; number of aphids, positively determining predator presence; and number of ants farming the colony, which negatively influenced the presence of aphid predators (Table 3.3, Figure 3.2).

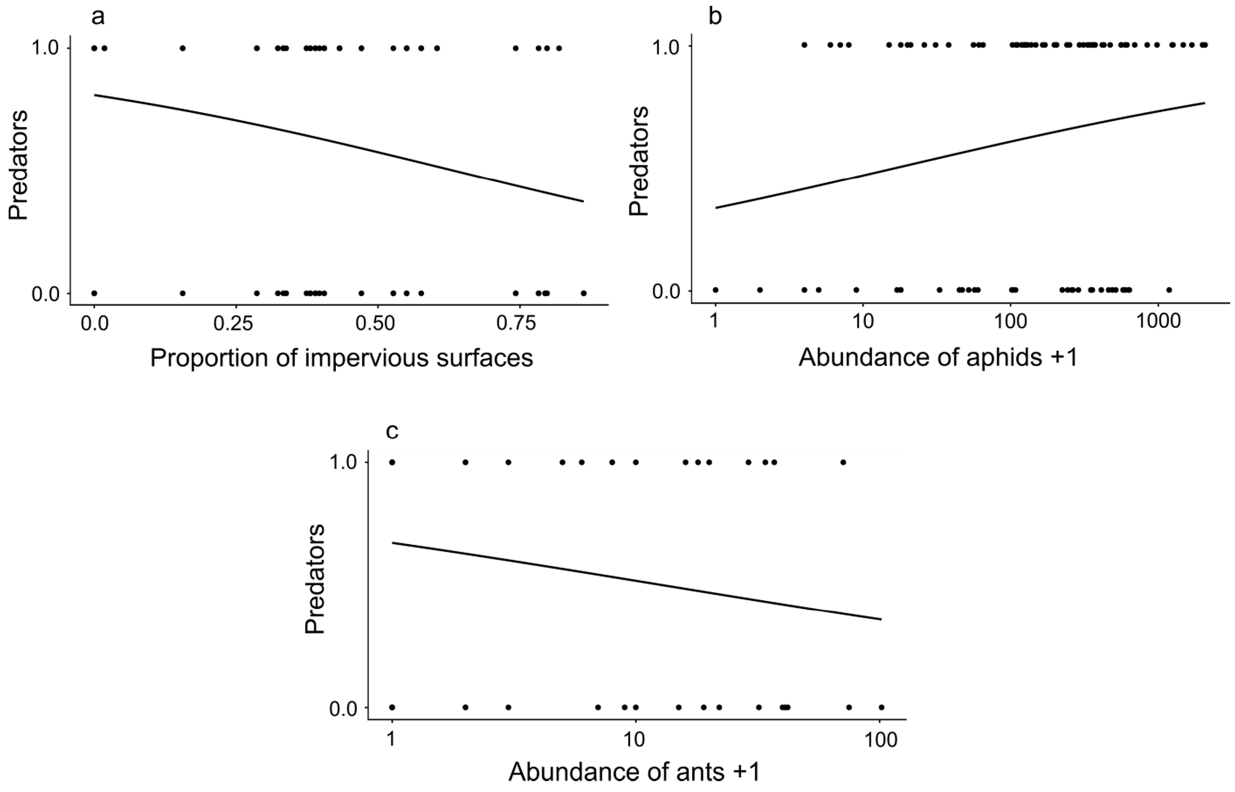


FIGURE 3.2. Representation of logistic regression models of (a) proportion of impervious surfaces, (b) number of aphids and (c) number of ants farming aphid colonies in predicting the presence (1) or absence (0) of predators in the colonies. Note that a multivariate logistic mixed effects model was used (see methods), however the trend line for a logistic regression model for just one explanatory variable on each panel was used to illustrate the direction of relationship between variables. Log scale used on x axis of panel (b) and (c).

3.3.3 ANTS FARMING APHID COLONIES

Three candidate models were selected based on AIC differences for explaining the presence of ants farming aphid colonies (Table 3.2, models 6, 7, 8). Model 7 (Table 3.3), with number of aphids, predators and parasitized mummies as explanatory factors, seems to be the best model due to its higher Akaike weight (0.434). However Figure 3.3 only shows the logistic regression curves for number of aphids (positive; Fig 3.3a) and number of predators (negative; Figure 3.3b) as explanatory factors since the number of parasitized mummies was not significant at α = 0.05 (Table 3.3, model 7).

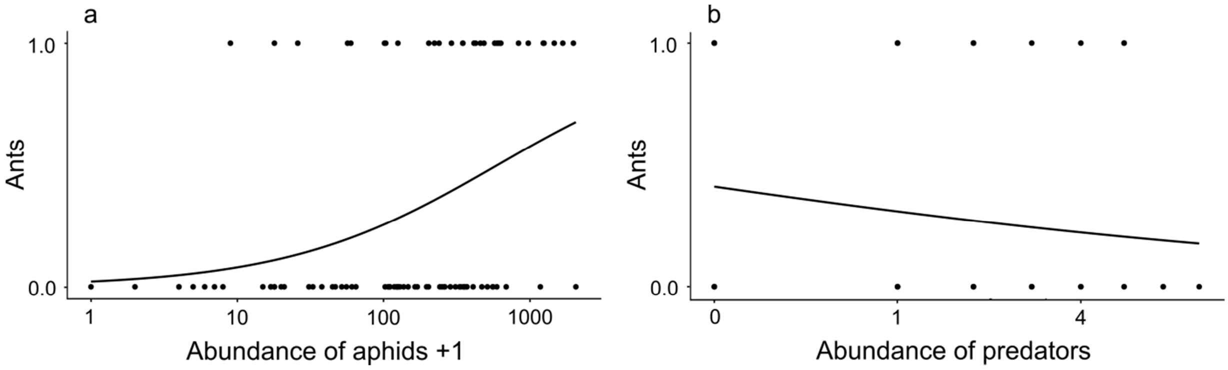


FIGURE 3.3. Panel (a) shows the logistic regression curve for number of aphids as an explanatory variable for the presence (1) or absence (0) of ants farming aphids on the experimental plants. Panel (b) shows the logistic regression curve for number of predators predicting number of ants farming aphid colonies. Note that a multivariate logistic mixed effects model was performed (see methods), however the trend line for a logistic regression model for just one explanatory variable on each panel was used to illustrate the direction of relationship between variables. Log scale was used on axis x on panel (a) and squared-root scale on panel (b).

3.3.4 PARASITOID ATTACK

Two candidate models were selected for explaining the presence of parasitized aphids on the colonies; first with the numbers of aphids, colony-farming ants and distance to the town center, and second with the first two variables but without distance to the town center (Table 3.2, models 9 and 10). Since distance to the town centre was not significant in model 9 (Table 3.3) we considered the model with only the numbers of aphids and colony-farming ants as the best overall model (model 10 in Table 3.3, Figure 3.4). Both variables were positively correlated with the presence of parasitized aphids on the experimental colonies.

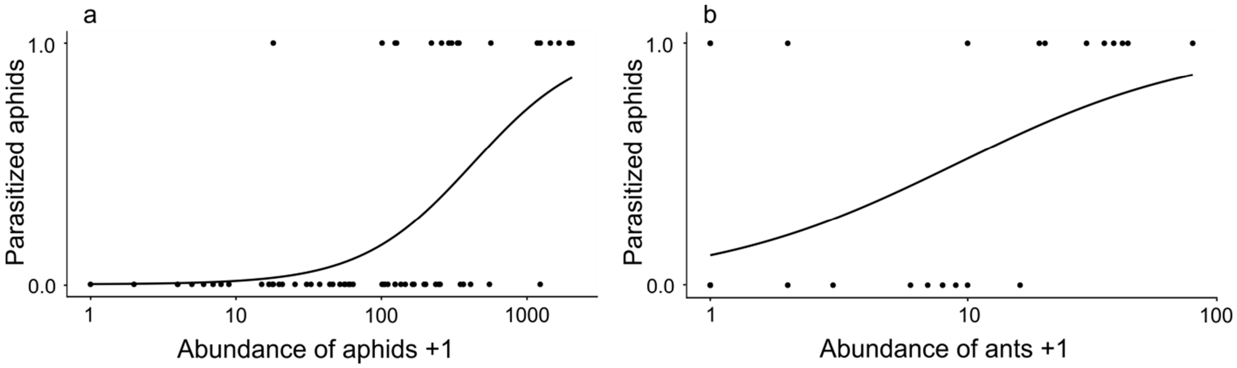


FIGURE 3.4. Panel (a) shows the logistic regression curve for number of aphids as explanatory variable for presence (1) or absence (0) of mummies on the experimental plants. Panel (b) shows the logistic regression curve for number of ants farming the colonies predicting number of parasitized aphids. Note that a multivariate logistic mixed effects model was used (see methods), however the trend line for a logistic regression model for just one explanatory variable on each panel was used to illustrate the direction of relationship between variables. Log scale used on x axis of both panels.

3.4 DISCUSSION

Our aim was to investigate how urbanisation may affect the intensity and outcome of interactions between species at higher trophic levels, using the black bean aphid, its natural enemies and ant mutualists as a model system. Overall, we found that the presence of mutualistic ants, predators and parasitoids varied as a function of aphid numbers on the plants. Predators was the only trophic level affected by abiotic factors, with fewer predators found in areas with increased proportions of impervious surfaces. The presence of mutualistic ants was associated with an increase in both aphid and parasitoid numbers, and a decrease in numbers of aphid predators. In no case did local plant diversity or distance to the urban centre affect the abundance of any of the interacting species.

We found that *Aphis fabae* colony size was not affected by abiotic variables, something expected as each colony remained on the study sites for a limited amount of time (~20 days for each sampling period), feeding on plants previously sown under identical conditions. This allows us to consider interactions at higher trophic levels without the confounding effects of plant and prey quality. Herbivore performance is directly linked to general health of the plants present in the habitat (Coleman and Jones 1988, Dreistadt et al. 1990, Hanks and Denno 1993, Strauss 1997, Awmack and Leather 2002, Altieri and Nicholls 2003, Huberty and Denno 2004, Christie and Hochuli 2005, Pineda et al. 2013). The abundance of predators was significantly affected by aphid colony size, the number of ants farming aphid colonies and the proportion of impervious surfaces in the habitat. Density dependence in predation is a widely recognized factor (Sinclair and Pech 1996, Hixon and Carr 1997, Anderson 2001, Arditi et al. 2001, Holbrook and Schmitt 2002, Lima et al. 2002, Hixon and Jones 2005). In our experiment, ants attending aphid colonies greatly reduced predator numbers. Previous studies have reported that honeydew-collecting ants can alter predator abundance (James et al. 1999, Wimp and Whitham 2001, Kaplan and Eubanks 2002). Neither of the above factors are unexpected. However, we also show that increased urbanisation, measured as the proportion of impervious surfaces surrounding the field sites, was associated with a reduction in the numbers of predators recorded.

Insect predators are relatively generalist, and their abundance will be associated with the local population size of a range of prey species. Given the reduction in native plant diversity and abundance in urbanised areas (Dreistadt et al. 1990, Burton et al. 2005, Williams et al. 2005, Williams et al. 2008, Isaacs et al. 2009, Walker et al. 2009, Williams and Winfree 2013), it would be surprising if predators were not sensitive to urbanisation (Zapparoli 1997, McKinney 2006, Jones and Leather 2012). Urban management techniques such as treading, bird feeding, mowing and pesticide application have been shown to negatively impact predacious beetles and hemipterans (Morris and Rispin 1987, Dreistadt et al. 1990, Helden and Leather 2004, Jones and Leather 2012, Bennett and Lovell 2014). It is known that human disturbances are often more detrimental towards higher trophic levels (Pauly et al. 1998, Jackson et al. 2001, Duffy 2002, Byrnes et al. 2005), and that extirpations of even one or two species that belong to higher trophic levels can cause cascading effects on species present on basal trophic levels (Paine 2002, Schmitz 2003) and critically affect ecosystem processes (Tilman et al. 1997, Byrnes et al. 2005, Hooper et al. 2005).

Urbanised environments might affect organisms at higher trophic levels more than their hosts or prey, particularly when they exhibit higher levels of resource specialization (Kruess and Tscharntke 1994, Tscharntke et al. 1998, Bailey et al. 2005, Pereira-Peixoto et al. 2016). In our study system, this may apply to insect predators but does not appear to affect the likelihood of colonies suffering parasitoid attack. While there was an indication that parasitized mummies were less frequently found on more urbanised sites of the gradient (closer to the town center, Table 3, model 9), this factor was not statistically significant.

There have been studies which found negative correlation between parasitism and urbanisation in a landscape context (Gibb and Hochuli 2002, Bennett and Gratton 2012, Calegaro-Marques and Amato 2014), which was not our objective in this work. The presence of physical barriers and structures like buildings and roads in cities might make insect dispersal problematic, and present an obstacle for breeding and foraging (Wratten et al. 2003, Raupp et al. 2010, Peralta et al. 2011). On the other hand, vegetated areas bordering roads, pavements, and streets might serve as habitats and "biological corridors", particularly the ones that maintain higher plant diversity and density (Haddad et al. 2003, Peralta et al. 2011). Bennett and Gratton (2012) found that parasitoid abundance in Wisconsin was positively correlated to local flower diversity, and this pattern occurred in areas containing moderated to high levels of urbanisation, their finding suggests that parasitoids can benefit from the increased availability of floral resources in urban environments, while the same trend was not found in rural sites.

We found that the mutualistic relationship between aphids and ants was responsible for a significant increase in aphid numbers. In our study, ant attendance at aphid colonies was not affected by habitat variables, and ant attended colonies were present even on the most urbanised sites of the gradient. Mutualistic ants of aphids are known to protect aphid colonies from predator attack, to prevent mould growth when honeydew accumulates and to avoid aphid competition with other herbivores on the same resource (Way 1963, Messina 1981, Ito and Higashi 1991, Floate and Whitham 1994, Stadler and Dixon 1998, Kaplan and Eubanks 2002, Kaneko 2003, Yao 2014). The relationship between aphids and tending ants can then confer direct benefits to aphid survival, allowing highest feeding rates and nutrient uptake; and at the same time, aphid-derived honeydew constitutes a nutrient-rich food that may be essential for the survival and growth of ant colonies (Kaplan and Eubanks 2002, Tegelaar et al. 2013). Aphid parasitoids are less likely to be affected by the presence of ants on aphid colonies than predators; although parasitoid wasps can sometimes be repelled by ants, once wasps successfully oviposit in aphids, these parasitized aphids frequently also receive ant protection, which might in turn result in higher parasitoid emergence rates (Völkl 1992, Kaneko 2002, Yao 2014). Such patterns (a negative effect of ant presence on generalist predators, a positive effect on specialist enemies) was found by Wimp and Whitham (2001), who examined the mechanisms that determined arthropod community structure in a riparian zone dominated by cottonwood. Urban ecosystems seem to show similar trends.

Overall, only predators were affected by the features of urbanisation measured on our study. This influence of environmental disturbance on multi-trophic interactions in urban habitats could result in important consequences for the assembly of local ecological communities, and also direct and practical implications for biocontrol services that natural enemies provide on these habitats (Kruess and Tscharntke 1994, Gibb and Hochuli 2002, Eubanks and Finke 2014, Calabuig et al. 2015). For example, Turrini et al. (2016) investigated the effects of urbanisation on trophic interactions, and found that predators reduced aphid abundance less in urban than in agricultural ecosystems. This reduction in top-down regulation in urban areas resulted in plants having reduced biomass, when compared to plants in adjacent agricultural areas. Finding such as these emphasize that urbanisation can influence not only interactions at higher trophic levels, but that these changes also affect plant communities through trophic cascades (Schemske et al. 1994, Brudvig et al. 2015).

Urban green spaces are of crucial importance for the quality of life of our increasingly urbanised society (Chiesura 2004), and are valuable elements in ecological networks, providing habitats for urban wildlife (Ignatieva et al. 2011). Our results highlighted the negative effect of the main characteristic of cities, the increase amount of impervious surfaces, on an important trophic guild. Given that the amount of impervious surfaces is highly negatively correlated with proportion of green areas, our results reinforce the importance of maintaining and increasing the quality of urban green spaces as habitats for the conservation of biological diversity (Botkin and Beveridge 1997, Peralta et al. 2011), and consequently also on trophic dynamics.

One of the major challenges of ecology is to understand and predict the consequences of environmental changes for biodiversity and ecosystem functioning (van der Putten et al. 2004, Hooper et al. 2005). Rapid human-induced changes affect interactions among trophic levels in complex ways (Harrington et al. 1999). Variation in responses within and between trophic groups may cause restructuring of communities through changes in competitive, bottom-up and top-down control effects (van der Putten et al. 2004). Any given species is affected at least to a certain degree by interactions with other species, therefore understanding how species interactions potentially affect food web structure and function in urban habitats might help us to succeed when planning conservation strategies (Faeth et al. 2005, Faeth et al. 2011). To our knowledge, our work presents the first effort to address how interrelated multitrophic interactions composed by herbivory, predation, parasitism and mutualism behave in urban habitats, with predation the most affected by the increase of urban features in the habitat. Our findings highlight the need for careful consideration of how patterns of species interactions may be modified in urban settings, which is crucial for the essential conservation efforts that will promote ecosystem services and functioning in cities.

Chapter 4 PATTERNS OF INSECT PREDATION AND MUTUALISTIC INTERACTIONS ARE AFFECTED BY URBANISATION

4.1 INTRODUCTION

Urbanisation modifies natural environments by transforming the landscape and significantly reducing local biodiversity (Beardsley et al. 2009, MacGregor-Fors et al. 2010, Reis et al. 2012). Urban development can eliminate high proportion of native species, and consequently increasing global extinction rates (Vale and Vale 1976, Luniak 1994, McKinney 2002, Van der Veken et al. 2004, Fattorini 2011, Scherner et al. 2013). One of the main causes is simply a species-area effect; with the substitution of natural systems by large parcels of sealed and impermeable areas, which reduces the habitat available for wildlife (McKinney 2008). This loss of local native species and the high variation in habitat structure and resource levels of cities also leads to disturbances of assemblages of interacting species in ways that remain largely unexplored (Faeth et al. 2005, Hagen et al. 2012).

For example, urban environments can modify the way species interact by altering host plant quality, availability and accessibility, also known as bottom-up factors, and also by altering abundance and diversity of natural enemies (top-down factors) (Thomas 1989, Kim 1992, Shrewsbury and Raupp 2006, Raupp et al. 2010). Interactions between predators and their prey are particularly predisposed to being disrupted by urbanisation (Raupp et al. 2010, Burkman and Gardiner 2014), and such changes may play an important role in determining how populations are regulated and communities structured (Rodewald et al. 2011, Fischer et al. 2012, Møller and Ibáñez-Álamo 2012).

The altered landscapes and modified habitats of highly urbanised environments (Rebele 1994, Jenerette and Wu 2001, Pickett et al. 2001) can present altered plant structure such as decreased density, host-plant availability, plant abundance and diversity -with lower numbers of native plants and higher numbers of exotic ones - (McDonnell and Pickett 1990, McIntyre 2000, Raupp et al. 2010). Management decisions and landscaping of commercial and residential urban areas are characterized by the constant removal of shurbs, herbs, wild plants and dead wood and introduction of grasses and ornamental exotic plants (Marzluff and Ewing 2001, Smith and Fellowes 2014, Smith et al. 2015). Plant composition and structure can strongly influence the assembly of communities of herbivores, and therefore will influence abundance, diversity and distribution of natural enemies (Shrewsbury and Raupp 2006, Smith and Fellowes 2014, 2015).

Other features of urban environments that can potentially have an effect on arthropods are hardscapes made of impermeable materials, which are largely used in constructions of buildings, roads and other sealed artificial structures (Raupp et al. 2010). Their amount and extent can vary greatly within and between cities, and their presence contributes to habitat fragmentation, microclimatic shifts (e.g. urban heat island), alteration plant-water relations and inhibiting or barring the movement of herbivores and their natural enemies (McDonnell and Pickett 1990, McIntyre 2000). However, even with their overall characteristics, urban ecosystems can contain patches with abiotic structure similar to natural habitats, where native biota can persist (Eversham et al. 1996, Hobbs et al. 2009, Lundholm and Richardson 2010). In most cities some native vegetation is still available within the urban matrix, mostly in parks and suburban gardens (Parsons et al. 2006), and their presence promote biodiversity and ecological services (e.g. pollination, nutrient cycling) if properly managed (Smith and Fellowes 2014, Smith et al. 2015).

However, still little is known about how the radically transformed habitats found in urban areas affects patterns of species interactions. Impacts from altered biotic and abiotic environment on species abundance and diversity are expected to arise when there are modifications of biotic interactions between enemies (e.g. predators, parasites, vector of diseases and competitors) or biotic resources or conditions (e.g. hosts plants, nesting and ovipositing sites, mutualists, microclimate) (Mooney et al. 2016). An assessment of the interplay between these factors is central to any understanding of how ecological communities are structured in urban areas, and how the degree of urbanisation affects the patterns observed. Populations of insect herbivores, such as aphids, can be used as a model system to address these questions.

Aphid populations are structured not only by a combination of top-down and bottom-up factors, but also by lateral factors (Wimp and Whitham 2001). Bottom-up effects are the consequence of variation in host plant diversity, quality and structure (Müller et al. 2005). Top down effects are the result of the action of natural enemies, such as parasitoids, coccinellid beetles and hoverflies (Hazell and Fellowes 2009). Lateral factors include the presence of mutualists; some aphid species are mymercophiles, tended and protected by ants in return for honeydew (Rotheray 1989). Each group of interactions may be affected by the changes seen in urban ecosystems, and teasing apart any resulting effects benefits from an experimental approach.

Here, we ask how patterns of predator-prey and mutualistic interactions are affected by urbanisation. We use two aphid species, the regularly ant-attended black-bean aphid *Aphis fabae* Scopoli (Hemiptera: Aphididae) (Völkl et al. 1999, Fischer et al. 2001, Fischer et al. 2005), and the non-ant attended pea aphid *Acyrthosiphon pisum* Harris (Hemiptera: Aphididae) (Engel et al. 2001), both reared on broad bean plants *Vicia faba* L. Colonies were placed on an urbanisation gradient in a large town in southern England, and we use this system to ask how urbanisation (land use, local plant richness) a) affects interactions with naturally occurring predators and b) interactions with the mutualistic ant species, *Lasius niger* L. and *Myrmica rubra* L. Sampling happened during two years with frequent visits to study sites (27 sites during the first year and 32 sites on the second year).

4.2 METHODS

4.2.1 STUDY AREA AND HABITAT VARIABLES

The study area is located in Greater Reading, Berkshire, England (51°27’N, 0°58’W). Reading is a large town with a population of 290 000, which covers an area of ca. 72 km^2 (Office for National Statistics 2013). For the first year of sampling, 27 experimental sites were studied (summer of 2015), and 32 sites were studied in the second year of sampling (summer of 2016). Study site selection was made in order to capture a gradient from very urbanised sites on the town centre to suburban areas located on the south, containing main habitats like parks, private gardens, churchyards, carparks, driveways, and woodlands. Each study site was at least 110 meters apart. Habitat variables were obtained using GIS, utilising the topography layer from the Ordnance Survey MasterMap®, at a scale of 1:1250. Thirty meters radius buffers were delimited in each study site, and a reclassification of vectors was made to result in proportions of area of the following habitat types within those buffers: gardens, which was composed of lawns and flower beds with ornamental plants and bushes; woodlands, composed of shrubs and trees (coniferous and non-coniferous); buildings (any building or artificial structures made of concrete, brick or stone) and roads (roads, roadsides, tracks or paths made of impervious surfaces such as asphalt), using QGIS 2.8.1 (QGIS Development Team 2015). Additionally, plant species richness within the 30 meters radius buffers of each study site was estimated by the count of plant morphospecies during the experiment.

4.2.2 STUDY SYSTEMS AND SUMMER RECORDING

Monoclonal cultures of *Acyrthosiphon pisum* Harris (the pea aphid, hereafter PA) and *Aphis fabae* Scopoli (the black bean aphid, hereafter BB) were maintained in a laboratory using plastic and mesh cages. Cultures were kept at a constant temperature of 20 ± 1 °C and 8:16 h light regime at ambient humidity on dwarf broad bean, *Vicia faba* L. (var. the Sutton dwarf). Three days before being allocated to the study sites, three adults from each aphid species were transferred from the monoclonal cultures and reared on cages containing 14-16 day old *Vicia faba* (18-22 cm tall), to allow the new colonies to get established. These plants were previously sown in pots with traditional potting compost (Vitax Grower, Leicester, England) in a Controlled Temperature Room at a constant temperature (20 ± 1 °C) and 8:16 h light regime, being watered as needed. After three days, one colony of PA and another one of BB on *Vicia faba* plants were placed at the study sites (60-80 cm apart). Two days after the experimental colonies were placed in the field, aphid, ant and predator numbers were recorded for the first time, and recording subsequently occurred every four days, for five recording events in total. At the end of this sampling period, colonies were returned to the laboratory and replaced by new ones in the field. Sampling was repeated four times in 2015 (sampling period one: May 16th, 20th, 24th, 28th and June 1st; period two: June 15th, 19th, 23th, 27th and July 1st; period 3: 16th, 20th, 24th, 28th of July and August 1st; period four: August 14th, 18th, 22th, 26th and 30th), and three times in 2016 (sampling period five: May 16th, 20th, 24th, 28th and June 1st; period six: June 16th, 20th, 24th, 28th and July 2nd; period seven: July 29th, and 2nd, 6th,10th and 14th of August).

4.2.3 DATA ANALYSIS

Statistical analyses were carried out using R 3.1.2 (R Development Core Team 2014). The dataset for analyses consisted of the cumulative numbers of aphids and the presence or absence of predators and ants along the five counting events on each of the seven sampling periods. Some colonies were lost during the experiment, caused by poor plant health or herbivory of plants by snails and slugs, and also through damage or theft by the public. This resulted in 183 observations for analysis of BB colonies and 177 observations for the PA colonies. To analyse PA and BB aphid colony numbers we applied separate linear mixed models fitted by reduced maximum likelihood using package nlme (Pinheiro et al. 2016), and as explanatory variables we used presence or absence of ants and predators, proportion of gardens, buildings, roads, and plant species richness. For these models and the following below we accounted for repeated sampling of the colonies through time by adding period as a random effect. We removed the variable proportion of woodlands from the set of explanatory variables due to its correlation with garden and roads (-0.66 and -0.61, respectively).

To investigate which factors determined the occurrence of predators and ants on PA and BB colonies we performed separate logistic regression mixed models with a binomial error distribution (with canonical link logit) using the function glmer of package lme4 (Bates et al. 2015), fitted by maximum likelihood (Crawley 2007). When modelling predators we used as explanatory factors the proportion of gardens, buildings, and roads, and plant species richness, number of aphids and presence or absence of ants. When modelling ants we used the same habitat variables, as well as controlling for aphid numbers on the colonies and the presence or absence of predators. Model selection was made by comparing models using Akaike's Information Criteria (AIC) by fitting the full model with the set of all explanatory variables and removing the least significant term on each step (refitting the model each time), until the optimal model (with the lowest AIC) is found (Crawley 2007, Bolker et al. 2009, Zuur et al. 2009). Counts of aphids were log-transformed to deal with extreme values and to standardize and homogenize model residuals.

We checked for collinearity between explanatory variables in our models through variance inflation factors (VIF) which is used as an indicator of multicollinearity in multiple regression, with VIF values higher than 3 indicating that covariation between predictors may impose a problem (Zuur et al. 2007). Our VIF values were in the range of 1.01-1.50. The response variables were checked for spatial autocorrelation through spline correlograms on package ncf (Bjornstad 2015), in which we did not find any significant spatial structure. We also confirmed the validity of models by checking normality, independence and homogeneity of model residuals.

4.3 RESULTS

In total, we observed 18490 PA aphids and 46804 BB aphids, 377 PA predators and 374 BB predators, 244 ants preying on PA colonies and 1555 mutualistic ants on BB colonies (Figure 4.1). Both *Myrmica rubra* (L.) and *Lasius niger* (L.) were found on PA and BB colonies. In addition to ants, predators of PA were mainly spiders (Arachnida; 61.8%) and hoverfly larvae (Diptera: Syrphidae; 27.32%), and in smaller numbers of ladybirds (Coleoptera: Coccinellidae; 3.18%), aphid midge larvae (Cecidomyiiidae; 2.91%), harvestmen (Arachnida; 1.59%), flower bugs (Hemiptera: Anthocoridae; 1.32%), earwigs (Dermaptera: Forficulidae; 1.06%), lacewings (Neuroptera; 0.53%) and assassin bug (Hemiptera: Nabidae 0.26%). Predators of BB were mainly spiders (Arachnida; 55.88%) and hoverfly larvae (Diptera: Syrphidae; 22.46%), and also aphid midge larvae (Cecidomyiiidae; 8.02%), ladybirds (Coleoptera: Coccinellidae; 6.15%), lacewings (Neuroptera; 2.41%), harvestmens (Arachnida; 1.87%), flower bugs (Hemiptera: Anthocoridae; 1.34%), earwigs (Dermaptera: Forficulidae; 1.34%) and ground beetles (Carabidae; 0.53%). Parasitized aphids were found only in negligible numbers (not found on PA colonies and only found on period 3, 4 and 7 on BB colonies in a few study sites) and therefore were not considered on analysis. The proportion of habitat elements and its maximum and minimum values are shown in Table 4.1.

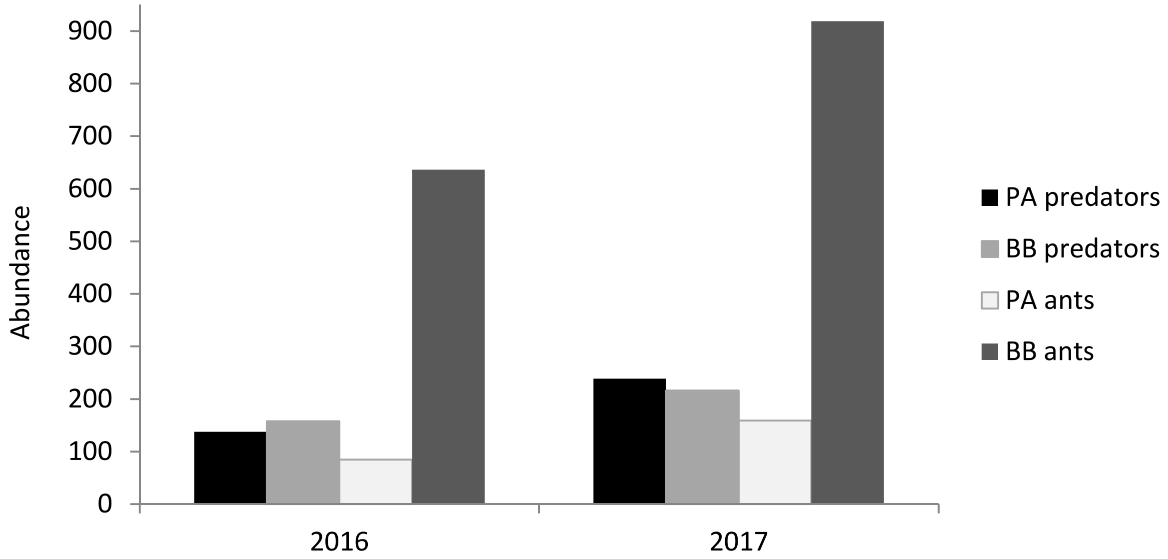


FIGURE 4.1. Total abundance of predators and ants found on *Acyrthosiphon pisum* colonies (PA) and *Aphis fabae* colonies (BB) according to year of sampling.

TABLE 4.1. Mean proportion (± SE) and range values of habitat elements within 30 meter buffers of the study sites.

	Plant richness	**Roads**	**Buildings**	**Woodland**	**Gardens**
Mean (±SE)	34.90 ± 1.24	0.287 ± 0.014	0.122 ± 0.008	0.191 ± 0.024	0.349 ± 0.016
Range	14 - 100	0 - 0.774	0 - 0.463	0 - 1	0 - 0.719

4.3.1 INFLUENCE OF HABITAT ON SPECIES INTERACTIONS

Numbers of predators were positively correlated with aphid numbers, suggesting a density dependent relationship. The presence of predatory ants did not affect PA numbers, while the presence of mutualistic ants was associated with significantly increased numbers of BB. Habitat features did not significantly affect aphid numbers (Table 4.2, models 1 and 2). The presence of ants negatively affected the likelihood of finding predators on colonies of both aphid species. Fewer BB predators were found in areas with a higher proportion of roads, and an increased proportion of buildings in the habitat negatively affected the presence of predators, but positively affected the numbers of predatory ants, found on PA colonies (Table 4.2, models 3, 4 and 5). Increased numbers of mutualistic ants on BB colonies were associated with increased BB colony size, higher local plant species richness and higher proportions of roads in the study sites. The presence of predators was negatively associated to the presence of mutualistic ants found on BB colonies (Table 4.2, model 6).

TABLE 4.2. Summary of models predicting abundance of *Aphis fabae* (BB) and *Acyrthosiphon pisum* (PA) and the occurrence of predators and ants found on colonies of each aphid species as response variables, and proportion of habitat types, plant richness and aphid species, predators and ants as explanatory variables. AIC values for each model are given. Models with significant explanatory factors are shown in bold.

Model ID	**AIC**	**Response variable**	**Explanatory variable**	**Coefficient value ± SE**	**P**
1	304.6	**PA aphid**	Intercept	1.103 ± 0.196	0.0000
			Presence of predators	0.556 ± 0.090	0.0000
			Proportion of buildings	0.549 ± 0.346	0.1152
2	279.4	**BB aphid**	Intercept	1.862 ± 0.185	0.0000
			Presence of predators	0.188 ± 0.078	0.0165
			Presence of ants	0.440 ± 0.078	0.0000
			Plant richness	-0.003 ± 0.002	0.1151
			Proportion of buildings	0.557 ± 0.316	0.0796
3	182.9	**PA predators**	Intercept	-1.101 ± 0.551	0.0457
			PA aphid	1.664 ± 0.551	0.0000
			Presence of ants	-1.341 ± 0.502	0.0076
			Proportion of buildings	-3.320 ± 1.743	0.0568
4	212.2	**BB predators**	Intercept	0.342 ± 0.638	0.5920
			BB aphid	0.790 ± 0.316	0.0124
			Presence of ants	-1.119 ± 0.407	0.0060
			Proportion of roads	-2.120 ± 0.926	0.0221
5	163.3	**PA ants**	Intercept	-1.545 ± 0.420	0.0002
			Presence of predators	-1.147 ± 0.450	0.0108
			Proportion of buildings	5.169 ± 1.682	0.0021

6	279.4	**BB ants**	Intercept	-6.627 ± 1.229	0.0000
			BB aphid	2.087 ± 0.419	0.0000
			Presence of predators	-0.888 ± 0.408	0.0294
			Plant richness	0.036 ± 0.011	0.0015
			Proportion of roads	2.042 ± 1.013	0.0438

4.4 DISCUSSION

Our objective in this study was to ask how habitat changes associated with urbanisation may alter patterns of interactions between insect herbivores, their predators and mutualistic ants. We controlled for habitat associated variation in plant quality and initial aphid colony size, allowing us to disentangle effects resulting from changes in the presence of natural enemies and mutualistic ant species. Local habitat factors (human-constructed surfaces, local plant species richness) did not affect aphid colony size, but the presence of ant mutualists was associated with an increase in numbers of black bean aphids. The presence of ants was associated with a reduction in insect predator occurrences, and both assemblages were more likely found on larger aphid colonies. Predator occurrences were reduced at study sites with higher proportions of roads (BB) and buildings (PA). However, ants showed the inverse pattern, where increased numbers of predatory ants (PA) were associated with an increased proportion of buildings, and attendance of BB colonies by mutualistic ants was positively associated the proportion of roads and plant species richness. This suggests that anthropogenic changes associated with urbanisation may considerably alter the structure of local ecological assemblages, with some taxa (predatory and mutualistic ants) benefiting more than others (insect predators).

Roads can affect ecological interactions in different ways, such as by modifying animal movement and dispersal, or by altering local physical environment (Trombulak and Frissell 2000). For example, heat stored on road surfaces is stored and then released into the atmosphere at night, creating heat islands (Asaeda and Ca 1993, Trombulak and Frissell 2000), and also the deposition of pollutants from roads generally contains heavy metals and de-icing agents (Getz et al. 1977, Richard and Alexander 1998), both of which may affect fitness and survival of terrestrial species. Fundamentally, roads can act as barriers or filters to animal dispersal (Richard and Alexander 1998), with studies finding that carabid beetles and wolf spiders are blocked by roads as narrow as 2.5 m wide (Mader 1984). Furthermore, the quantity and extent of impervious cover (paved surfaces structures such as buildings and roads) cause strong detrimental effects on arthropod diversity and abundance (Morse et al. 2003, Sadler et al. 2006, Magura et al. 2008, Bennett and Gratton 2014), including natural enemies such as parasitoids (Bennett and Gratton 2012).

However, predatory ants found on PA colonies and mutualistic ants found on BB colonies were positively associated with the proportion of roads and buildings in the habitat. This could be linked to ant habitat preferences. For example, fire ants (*Solenopsis invicta* Buren) are abundant in open habitats associated with human activity where the soil has been disturbed by agricultural practices, logging, roads and roadsides, where direct sunlight constantly reach the soil surface (Porter and Savignano 1990, Stiles and Jones 1998). Other studies have shown that urbanised areas might serve as habitat and corridors for dry-adapted and heat tolerant species such as ants (Gibb and Hochuli 2003, Menke et al. 2010, Menke et al. 2011). Others have reported that urban habitats tend to select opportunistic ant species which are highly competitive generalists, and also ants species that form large and aggressive territorial colonies (Carpintero et al. 2004, Lessard and Buddle 2005, Philpott et al. 2010). *Lasius niger* and *Myrmica rubra* live in colonies of about several thousand individuals, showing aggressiveness and displacement against competitors (Novgorodova and Gavrilyuk 2012, Garnas et al. 2014), both species are omnivores with varied diet which consists of honeydew, other invertebrates, pollen, seeds and human waste (Offenberg 2001, Czechowski et al. 2008, Servigne and Detrain 2008, Dussutour and Simpson 2012) and therefore are good candidates for being advantaged by the increased heterogeneity of resources of urban habitats (Slipinski et al. 2012). Given that ants are among the most prevalent and widespread predators in terrestrial ecosystems, and that many species that share the same trophic level can potentially compete with and prey upon each other (Halaj et al. 1997), the negative effect that we found of both predatory and mutualistic ants have at displacing other predator species on our experimental aphid colonies was perhaps not surprising, and have already been reported in other studies (Tilles and Wood 1982, Fischer et al. 2001, Phillips and Willis 2005, Novgorodova and Gavrilyuk 2012). Protection of food resources from other competitors and territoriality are key ant features, which permit colonies to maintain a stable flow of resources and consequently colony persistence (Novgorodova and Gavrilyuk 2012). In the work performed by Phillips and Willis (2005), were they presented aphid-attending ants with threats (i.e., aphid predator and competitor), resident ants invariably responded by attacking the intruder. Nevertheless, it might be advantageous to investigate with more detailed experimental work whether the benefits of pest suppression by ants outweigh the negative impact of ants on other predators.

Indirect interactions between ants and other natural enemies can be complex (Eubanks 2001), and in our study sites ants acted as predators on PA colonies, it displaced beneficial aphid predators of both aphid species, and acted as beneficial mutualists of BB aphids. Presence of mutualistic ants was positively correlated when the local habitat was more plant diverse, which may provide greater opportunities for mutualistic interactions with aphid colonies. This behaviour could be linked to the fact that ants not exclusively choose to just tend aphids or just prey on them, but yet whether ants “milk” the aphids for honeydew or eat them, as well the rate of attendance, depend upon the general levels of food available in the ants foraging areas (Rotheray 1989, Offenberg 2001, Nagy et al. 2013). On initial studies about this theme, it was suggested that ants would keep a balanced ratio between carbohydrates and proteins when feeding, and would initiate predation on attended aphid colonies when other prey and protein food sources were poor (Pontin 1958). Although the work by Offenberg (2001) did not supported Pontin’s hypothesis - who observed that when offered alternative sugar, the direction of the mutualistic interaction moved to predation, and the offering of alternative prey had no significant effect – their work was not performed on “real life” habitats but on controlled laboratory environment where only three different alternative prey were offered. The fact that ants with predatory behaviour against PA aphids were more likely found on highly urbanised habitats with increased proportion of buildings also indicate an increased need for prey and protein rich food sources to ants on highly urbanised environments.

Very little attention is paid to the effects of habitat structure of cities in determining trophic dynamics and species interactions. Our data suggests that such variables play a major role for predatory and mutualistic interactions, with likely consequences for the structure of urban insect communities. The abundance of aphids was not affected by urban habitat structure, but it is important to note that this was a deliberate consequence of experimental design; uniclonal - aphid clones can vary in response to host plants and in resistance to natural enemies (Collins et al. 2001, Hazell and Fellowes 2009) - aphid colonies were exposed for a limited amount of time, with host plants previously sown and grown in pots on the same soil compost and environmental conditions. Although this allowed us to observe interactions at higher trophic levels without the confounding effects of plant quality, it limited our ability to detect notable environmental effects on herbivore population numbers. Nonetheless, the effect that the main habitat features of highly urbanised habitats (higher proportion of buildings and roads) on trophic structure detected on this work is clear. The reduction in predator occurrence, with a concurrent increase in ant presence, could also lead to a potential increase in populations of ant-attended pest species. This may impact the environmental services predators provide (Olden et al. 2004, Vincent et al. 2007).

Arthropods in cities are crucial for many ecosystem services, such as the pollination of plants (essential in urban agriculture), nutrient cycling, the decomposition of waste and decaying matter, and biocontrol performed by parasitoids and predators (Alberti et al. 2003, Faeth et al. 2005). Therefore it is of great importance that the proper management of public and private land in cities takes into account the arrangement of features and habitat structure potentially able to benefit arthropods, promoting and supporting their conservation (Smith et al. 2015). We suggest that urban ecosystems present a fascinating opportunity for ecologists to explore the complex interplay between enemies and mutualists in changing environments.

Chapter 5 RESPONSE OF PREDATORS' FUNCTIONAL GROUPS TO URBAN GREEN SPACES

5.1 INTRODUCTION

Urban green spaces provide a range of essential environmental services to human populations and wildlife, and therefore are an essential and crucial part for the provision of quality of life in any city (Bolund and Hunhammar 1999, Tratalos et al. 2007, James et al. 2009), and can be defined as any vegetated land or water within or adjoining an urban area (Swanwick et al. 2003). The amount, structure, composition and spatial configuration of green spaces will influence their quality and ecological function as habitat (Bolund and Hunhammar 1999, Pauleit and Duhme 2000, Whitford et al. 2001, Turner et al. 2005, Niemelä 2014). These ecological services include the provision and maintenance of resilient species interactions, community and population dynamics, pest control, plant pollination and many others (James et al. 2009). Urban green spaces can also provide crucial environmental services such as buffering carbon emissions and air pollution (Hutchings et al. 2012, Strohbach et al. 2012), rainwater drainage (Bolund and Hunhammar 1999), the regulation of microclimates (Millward and Sabir 2011), and provision and support of bio-geophysical cycles and processes (e.g. nutrient cycling and decomposition) (James et al. 2009, Wolch et al. 2014).

One of the most important consequences of urbanisation is biotic homogenisation, which is likely to result in negative impacts on ecological communities, with various genetic, functional and evolutionary consequences (Olden et al. 2004, Filippi-Codaccioni et al. 2009). Human-induced environmental changes and disturbances might act as a filter, selecting from a potential pool of species the ones that are able to survive and thrive in novel ecosystems (Smart et al. 2006, Devictor et al. 2008, Lowe et al. 2016). Urbanisation is frequently found to be a homogenising agent of urban wildlife, leading to a decreased abundance of specialist species (Kitahara et al. 2000, McKinney 2006, Devictor et al. 2008, Sorace and Gustin 2009). The main causes of urban biotic homogenisation can be attributed to habitat changes, reduced resources, and new or altered biotic interactions that can make it difficult for many species to persist (McKinney 2002, Shochat et al. 2010, Lowe et al. 2016). This effect could be particularly significant for organisms that belong to higher trophic levels, which exhibit increased resource specialization (Kruess and Tscharntke 1994, Tscharntke et al. 1998, Bailey et al. 2005, Pereira-Peixoto et al. 2016).

Predators frequently show a higher degree of sensitivity to urbanisation and the environmental disturbances that arise from habitat alteration (Zapparoli 1997, Gibb and Hochuli 2002, Chapters 2, 3 and 4, McKinney 2006, Sattler et al. 2010b, Jones and Leather 2012, Burkman and Gardiner 2014, Turrini et al. 2016). Given the reduction in native plant diversity and abundance in urbanised areas (Dreistadt et al. 1990, Burton et al. 2005, Williams et al. 2005, Williams et al. 2008, Isaacs et al. 2009, Walker et al. 2009), it would be surprising if predators were not sensitive to the presence and size of green spaces within the urban matrix, as they are expected to be directly linked to the occurrence of potential prey species (McIntyre 2000, Raupp et al. 2010). Specialist predators, species that evolved to prey on a specific or limited range of prey, are potentially the best study systems available to test their degree of susceptibility to disturbances, and also the suitability of urban green spaces as its habitats. In contrast, generalist predators, with broad dietary and habitat requirements, are thought to respond positively to (or are not affected by) anthropogenic resources (McKinney 2002, Prange and Gehrt 2004, Burkman and Gardiner 2014).

Aphid predators have often paved the way forward in research on predation (Chambers et al. 1983, Rotheray 1989, Losey and Denno 1998, Lucas et al. 1998, Weisser et al. 1999, Wimp and Whitham 2001, Fox et al. 2004, Rand and Louda 2006, Straub and Snyder 2006, Ximenez-Embun et al. 2014, Turrini et al. 2016). Being common and easily observed in the field, aphid predators are of two types. Obligatory or aphid-specific predators depend on aphids for food. Included in this group are ladybirds (Coleoptera: Coccinellidae), many hoverflies (Diptera: Syrphidae), aphid midges (Cecidomyiiidae), lacewings (Neuroptera), flower bugs (Hemiptera: Anthocoridae) and some solitary wasps and other flies Rotheray (1989). The second group are facultative or polyphagous predators in which aphids are just part of a much wider diet, such as birds, ground (Carabidae) and rove beetles (Staphylinidae), social wasps (Hymenoptera: Vespidae), earwigs (Dermaptera: Forficulidae), and various groups of predatory flies. Taking this specific system into consideration, we could predict that by evaluating the response of the whole community of predators that prey on a particular prey, and classifying it according to the specificity of their dietary breadth in relation to that prey, could provide us significant insights of the effects of urban greenspaces on predatory trophic guilds. This avoids the potential biases and confounding effects associated with sometimes arbitrary specialist/generalist classifications, which are based on groupings of predator dietary breadth in relation to a wide range of potential prey present in a biological community

(Suarez and Case 2002, Attum et al. 2006, Mennechez and Clergeau 2006, Rand and Tscharntke 2007).

A limited number of studies have demonstrated that an examination of arthropod predators can provide a significant understanding into the local and regional factors that could potentially affect the function and structure of urban ecosystems (Peralta et al. 2011, Bennett and Gratton 2012, Bennett and Lovell 2014, Burkman and Gardiner 2014, Lowe et al. 2016, Pereira-Peixoto et al. 2016). This way, a greater comprehension of the relationship between functional traits of sensitive trophic guilds to the amount of urban green spaces could provide us valuable knowledge, which could potentially guide conservation practices that enhance biodiversity in cities (Bennett and Lovell 2014). In this work, our aim is to investigate changes in the abundance of several predatory species of widespread and frequent pests (the aphids *Acyrthosiphon pisum* Harris and *Aphis fabae* Scopoli) along an urbanisation gradient. There are surprising very few studies about aphids on a urban context, but *Aphis fabae* is known to have its population growth stimulated by air pollution (Dohmen et al. 1984, Flückiger 1987), and *Acyrthosiphon pisum* was found to be negatively affected by artificial light at night due to bottom-up effects on its host plant (Bennie et al. 2015), therefore the potential variation on herbivore fitness due to changes on its habitat in a urban ecosystem is likely to play an effect also on the community of predators that feed on them. Sampling occurred during two years with frequent visits to experimental colonies on study sites (27 sites during the first year and 32 sites in the second year), in Reading, UK. Both species are known to suffer heavy predation by many natural enemies (Rotheray 1989, Losey et al. 1997). We hypothesized that numbers of specialist predators will be correlated to an increased proportion of urban green spaces in the habitat, whereas the abundance of generalist predators should not be affected.

5.2 METHODS

5.2.1 STUDY SITES AND HABITAT VARIABLES

The study area is located in Reading (51°27’N, 0°58’W), Southern England, which has a population of 290000, and covers an area of ca. 72km^2 (Office for National Statistics 2013). Study sites were chosen in order to represent a gradient ranging from very urbanised sites in the town centre to suburban areas located on the south. The study sites contained urban habitats such as parks, private and public gardens, driveways, woodlands, churchyards and car parks. Twenty-seven sites were studied in 2015, and thirty-two in 2016. The habitat variables of each study site were obtained using the topography layer from the Ordnance Survey MasterMap®, at a scale of 1:1250. Performing GIS techniques on QGIS 2.8.1 (QGIS Development Team 2015), thirty meters radius buffers were delimited in each study site, and a reclassification of the map was made to calculate proportions of green area within those buffers, and this comprised of gardens and/or woodlands. Gardens were composed of flowerbeds (which usually contained ornamental plants and bushes) and associated lawns and grass. Woodlands were composed of shrubs and trees (coniferous and non-coniferous).

5.2.2 SUMMER RECORDING OF APHID PREDATORS

Monoclonal cultures of both *Acyrthosiphon pisum* Harris and *Aphis fabae* Scopoli were maintained in laboratory using plastic and mesh cages on dwarf broad bean, *Vicia faba* L. (var. the Sutton dwarf), and were kept at a constant temperature of 20 ± 1 °C and

8:16 h light regime at ambient humidity. Three days before being allocated to the study sites, three adults from each aphid species were transferred from the monoclonal cultures and reared on cages containing 14-16 days old *Vicia faba* (18-22 cm tall), to allow the new colonies to get established. After this period, one colony of each aphid species on *Vicia faba* plants was placed at each study sites. Two days after the experimental colonies were allocated, aphid and predator numbers were recorded for the first time. From that time point, recording subsequently occurred every four days, for five recording events in total. At the end of this sampling period, colonies were returned to the laboratory and replaced by new ones in the field. Sampling occurred during two sampling periods in 2015 (first: May 16th, 20th, 24th, 28th and June 1st; second: June 15th, 19th, 23th, 27th and July 1st); and also for two sampling periods in 2016 (first: May 16th, 20th, 24th, 28th and June 1st; second: July 29th, and 2nd, 6th, 10th and 14th of August).

5.2.3 ANALYSIS

All statistical analyses were performed using R 3.1.2 (R Development Core Team 2014). Predators found on both aphid colonies were summed together and classified according to Rotheray (1989) into specialists (or obligatory aphid predators) and generalists (or facultative aphid predators). Ladybirds, lacewings, flower bugs, aphid midges and hoverfly larvae were considered as specialist aphid predators; and earwigs, ground beetles, spiders and harvestmen were considered as generalist aphid predators. Ants were considered as a separate factor (presence or absence) on the study sites, as it can act as both predators of *Acyrthosiphon pisum* and as mutualists or predators of *Aphis fabae* (Offenberg 2001), and as observed in previous chapters, ants can negatively affect the occurrence of predators on aphid colonies. In order to obtain a meaningful quantitative response and avoid an excess of zeroes, the dataset of the two sampling periods in 2015 and the other two of 2016 were summed together. Additionally, some colonies were discarded from the dataset due to herbivory of plants by snails and slugs, poor health and damaging by the public, leaving 41 observations for analysis.

To address possible differences in abundance between numbers of specialist and generalist predators, we used a paired Wilcoxon signed-rank test. This test is a non-parametric alternative to a paired Student's *t* test, which can be used if the errors are non-normal (Crawley 2007). In order to assess the effect of urban green spaces on numbers of specialist predators a generalised linear mixed method (GLMM) fitted by maximum likelihood (Laplace Approximation), with a Poisson error distribution and a log link function was performed (Zuur et al. 2009), relating numbers of specialist predators to the proportion of greenspaces, occurrence of ants and mean number of aphids, using package lme4 (Bates et al. 2015). As numbers of generalist predators were over-dispersed, this variable was log transformed and then related to the proportion of greenspaces, occurrence of ants and mean number of aphids using a linear mixed effect model fitted by reduced maximum likelihood on package nlme (Pinheiro et al. 2016).

Year of sampling was considered as a random factor on both models, and mean numbers of aphids were log transformed in order to deal with extreme values and improve model convergence (Zuur et al. 2009). Model selection was done by model comparison using Akaike's Information Criteria (AIC) by fitting the full model with the set of all explanatory variables and removing the least significant term on each step (refitting the model each time), until the optimal model (with the lowest AIC) is found (Crawley 2007, Bolker et al. 2009, Zuur et al. 2009). For the model applied on generalist predators, model comparison with nested factors was always performed within models fitted by maximum likelihood, until the optimal model was found, which then was refitted by reduced maximum likelihood (Crawley 2007, Zuur et al. 2009).

We checked for presence of spatial autocorrelation in our response variables and model residuals through spline correlograms on package ncf (Bjornstad 2015), in which we did not find evidence of any significant spatial structure. We also confirmed the validity of models by checking normality, independence and homogeneity of model residuals.

5.3 RESULTS

In total, 238 generalist and 123 specialist predators were sampled, and 41782 aphids were observed. The ants *Myrmica rubra* L. and *Lasius niger* L. were found on the study sites (58% of the observations). Generalist predators were composed mainly by spiders (Arachnida; 94.54%), and in smaller amounts of earwigs (Dermaptera: Forficulidae; 2.94%), harvestmen (Arachnida; 1.26%), ground beetles (Carabidae; 0.84%) and assassin bugs (Hemiptera: Nabidae; 0.42%). Specialists predators comprised mostly of hoverfly larvae (Diptera: Syrphidae; 78.86%) and aphid midge larvae (Cecidomyiidae; 12.19%), and also of ladybirds (Coleoptera: Coccinellidae; 3.25%), flower bugs (Hemiptera: Anthocoridae; 3.25%) and lacewings (Neuroptera; 2.44%). The list of species found (apart from Arachnida) can be seen on Table 5.1. The proportion of green areas in study sites varied from 0.14 to 1 (mean ± SE: 0.54 ± 0.03).

TABLE 5.1. List of the predator species found on the experimental colonies and its trait classification of dietary breadth in regard to aphids.

Order - Family - Species	**Trait classification**
Diptera	
Syrphidae	
Episyrphus balteatus (De Geer)	Specialist
Eupeodes luniger (Meigen)	Specialist
Eupeodes corollae (Fabricius)	Specialist
Dasysyrphus tricinctus (Fallén)	Specialist
Syrphus ribesii (Linnaeus)	Specialist
Hemiptera	
Anthocoridae	
Anthocoris nemorum (Linnaeus)	Specialist
Anthocoris nemoralis (Fabricius)	Specialist
Nabidae	
Himacerus apterus (Fabricius)	Generalist
Neuroptera	
Chrysopidae	
Nineta vittata (Wesmael)	Specialist
Hemerobiidae	
Hemerobius lutescens Fabricius	Specialist
Diptera	
Cecidomyiidae	
Aphidoletes aphidimyza (Rondani)	Specialist
Coleoptera	
Coccinellidae	
Harmonia axyridis (Pallas)	Specialist
Harmonia quadripunctata (Pontoppidan)	Specialist
Propylea quatuordecimpunctata (Linnaeus)	Specialist
Carabidae	
Pterostichus madidus (Fabricius)	Generalist
Dermaptera	
Forficulidae	
Forficula auriculata Linnaeus	Generalist

The paired Wilcoxon signed-rank test showed that there was a significant difference in abundance between specialist and generalist predators (W = 538.5, Z = 2.38, P < 0.05, r = 0.37; Figure 5.1).

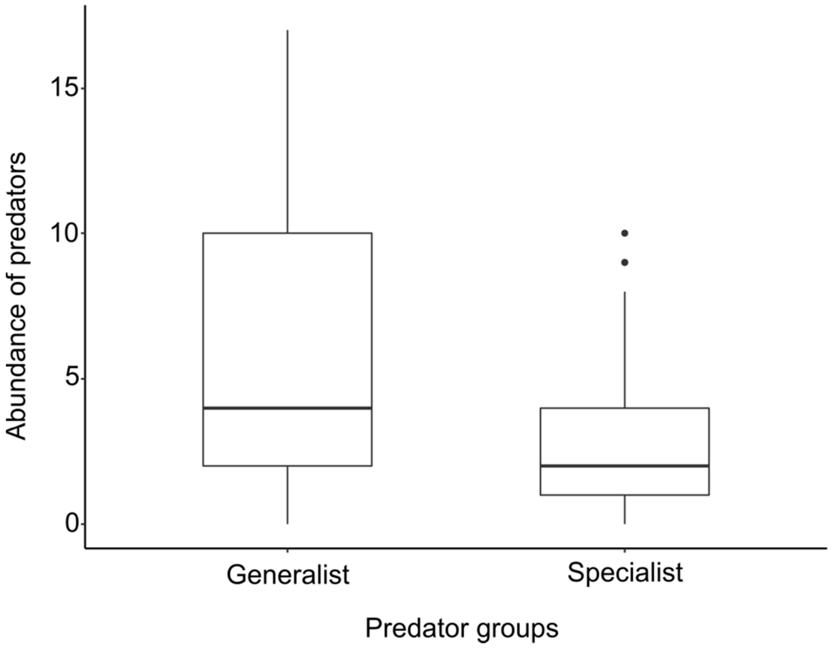


FIGURE 5.1. Boxplot showing the difference between numbers of predators classified as specialist or generalists aphid predators found on colonies of *Acyrthosiphon pisum* and *Aphis fabae* (lines within boxes represent the median values, top and bottom of boxes represent the first and third quartiles, whiskers are the lowest datum still within 1.5 IGR of the lower quartile, and the highest datum still within 1.5 IGR of the upper quartile, outliers are plotted as individuals points).

The best model in explaining the abundance of specialist predators had two positive and significant explanatory factors, the mean number of aphids and the proportion of green areas on the study sites (Table 5.2, model 1; Figure 5.2). The best model in explaining the abundance of generalist predators had only one variable, proportion of green areas on the study sites; however this factor was not statistically significant (Table 5.2, model 2).

TABLE 5.2. Summary of models predicting the abundance of specialist predators (model 1) and generalist predators (model 2) found on both *Aphis fabae* and *Acyrthosiphon pisum* colonies. AIC values for each model are given. Models with significant explanatory factors are shown in bold.

Model ID	AIC	Response variable	Explanatory variable	Coefficient value ± SE	P
1	199.3	Specialist predators	Intercept	-2.138 ± 0.915	0.019
			Mean number of aphids	0.969 ± 0.319	0.002
			Proportion of green areas	1.189 ± 0.391	0.002
2	41.8	Generalist predators	Intercept	0.499 ± 0.130	0.001
			Proportion of green areas	0.383 ± 0.224	0.096

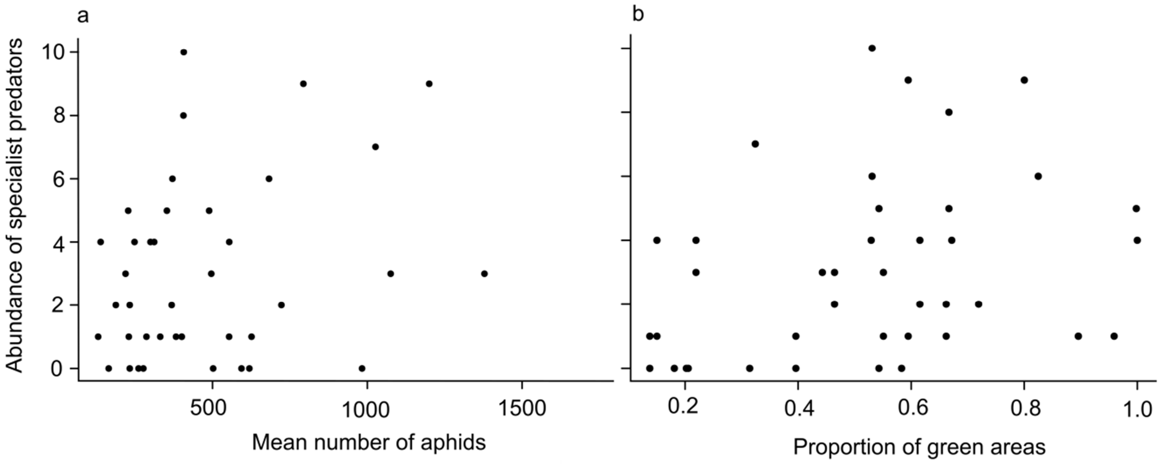


FIGURE 5.2. Abundance of specialist predators found on *Aphis fabae* and *Acyrthosiphon pisum* colonies according to abundance of aphids (a) and proportion of green spaces on study sites (b).

5.4 DISCUSSION

In this work, we wanted to investigate if the amount of green spaces in urban environments is an important environmental factor selecting species of specialist or generalist aphid predators. A difference between numbers of both groups was observed, and we confirmed our hypothesis that higher numbers of specialist predators are correlated to greater proportion of green areas in urban habitats, while generalist predators did not follow this trend. These findings are consistent with studies showing high sensitivity of monophagous and oligophagous species to urbanisation, habitat fragmentation and habitat loss (Kitahara and Fujii 1994, Posa and Sodhi 2006, Sorace and Gustin 2009, Bergerot et al. 2010, Lizée et al. 2011, Deguines et al. 2016).

Other than more particular prey species, specialist predators can present narrow tolerance limits and very specific habitat requirements, which would force them to depend and be restricted to certain habitat types (Kitahara and Fujii 1994). Although specialist predators, particularly aphid specialist predators, are well adapted to their host and tend to have higher searching efficiency (Snyder and Ives 2003, Toft 2005), they do not present the same persistence of a generalist predator (Symondson et al. 2002, Marvier et al. 2004), as generalists can subsist and reproduce on prey other than aphids (Toft 2005). Typical generalist traits (e.g. exploitation of more food types, broad tolerance limits, flexible habitat requirements) allow them to persist and thrive in more habitats and to be distributed widely and continuously (Kitahara and Fujii 1994, Kitahara et al. 2000, Marvier et al. 2004). As we have seen from our results, specialist predators were positively correlated with aphid colony size, but generalist predators did not show the same pattern. Snyder and Ives (2003) similarly showed that specialist natural enemies of *Acyrthosiphon pisum* exert density dependent control, in contrast to generalist predators. When the numbers of a predator species are strongly associated to a particular prey, as observed with some species of coccinelid beetles, Diptera and some species of hoverflies (Hassell and May 1986, Strand and Obrycki 1996, Snyder and Ives 2001, 2003), they can present many characteristics that are associated with increased prey location, close development or emergence time in relation to their main prey, and high reproductive potential (Turlings et al. 1990, Strand and Obrycki 1996, Snyder and Ives 2003). These traits have consequences for predator reproduction, as their life cycles are highly linked to its prey, so that they can respond in a density-dependent manner to changes in herbivore population numbers (Hanski et al. 1991, Bascompte and Solé 1998, Snyder and Ives 2001). However, these characteristics make them vulnerable to both habitat and resource fluctuations (Bascompte and Solé 1998, Nakagiri et al. 2001, Ryall and Fahrig 2006).

There is some discussion about the effectiveness of generalist predators in relation to specialists in biological control, where is argued that the predation efficiency of many generalist predator species while feeding on herbivores might be as (or more effective) than of a few specialist predator species, and that overall generalist predators are more abundant than specialist in most ecological systems (Sunderland 1999, Symondson et al. 2002, Fox et al. 2004, Rutledge et al. 2004). However, generalist predators alone are not good aphid suppressors, and most probably have a synergistic effect together with specialist natural enemies (specialist predators and parasitoids) (Snyder and Ives 2003, Toft 2005, Straub et al. 2008). Both groups play very different roles in aphid control and exert their effect in different phases of the aphid population cycle. The generalists can work as a preventive force against a potential outbreak, while the specialists might suppress a current outbreak (Snyder and Ives 2003, Toft 2005).

In our work we found that numbers of specialist predators were positively linked to the amount of local green space, but that numbers of generalists were not affected by the same variable. Some studies have found a constant number of generalist predators on gradients of human disturbance (Sorace and Gustin 2009, Gardiner et al. 2014), however others have found that generalists are even more abundant in cities than specialists (Lizée et al. 2011, Lowe et al. 2016). There is a strong theoretical belief that generalists and specialist predators would have distinctive responses associated to changes in habitat (Rand and Tscharntke 2007). Overall, environmental changes are expected to be more disadvantageous to specialist species in comparison to generalist species, as generalists are able to adapt more easily to varying habitat conditions (Clavel et al. 2011, Deguines et al. 2016).

In this work we did not expect to find differences in aphid abundance within study sites, given that initial abundance was controlled for and we did not assume that there would be a strong effect of urbanisation on aphid population growth rates, as herbivore performance is directly linked to general health of the plants present in the habitat (Coleman and Jones 1988, Dreistadt et al. 1990, Hanks and Denno 1993, Strauss 1997, Awmack and Leather 2002, Altieri and Nicholls 2003, Huberty and Denno 2004, Christie and Hochuli 2005, Pineda et al. 2013), and the host plants provided for our experimental colonies were previously sown under identical conditions. This allows us to consider interactions at higher trophic levels without the confounding effects of plant and prey quality. However, in regard to how urbanisation might affect abundance and diversity of naturally occurring aphids, Pautasso and Powell (2009) found that aphid biodiversity is positively correlated with human population size at a landscape scale in European countries, probably because human population size is associated with increased environmental productivity, species introductions, and habitat diversification. Within cities, aphids have been found to vary in abundance along a gradient of water availability and vegetation density, rather than level of urbanisation, and the authors suggest that aphids should be classified as urbanophiles (Andrade et al. 2017).

Species composition in urban areas is influenced by the presence and quality of many fine-scale habitats types within gardens, parks and other greenspaces, as well as the structuring and density of sealed areas (buildings, roads, and other impermeable structures), climate and frequency of disturbance (e.g. traffic intensity and pollution level) (Sattler et al. 2010a). The creation of landscapes of continuously smaller habitats and decreased connectivity between patches are already known causes of species extinctions (Didham et al. 1996, Harrison and Bruna 1999). Habitat patch size in urban environments seems to influence not only richness, but also species composition, with species at higher trophic levels more likely to be lost within smaller habitat patches (Gibb and Hochuli 2002). Specialist predators in particular are often considered to be linked to the presence of habitats utilised by their prey, consequently, loss of prey habitat would also mean reduction of predator habitat (Sutherland and Anderson 1993, Bascompte and Solé 1998, Swihart et al. 2001, Ryall and Fahrig 2006). Thus specialist aphid predators may particularly benefit from the increased amount of potential habitat promoted by the presence of urban green spaces.

Biotic homogenization generally arises from simplification of biological communities, and the loss of specialist species and their replacement by a few abundant generalists is regarded as a possible mechanism behind this pattern (Olden and Poff 2003, Gagne and Fahrig 2011). There is empirical evidence that the dampening of herbivore outbreaks is better promoted in habitats that can support a wider array of natural enemies, from generalist to specialist predators (Losey and Denno 1998, Cardinale et al. 2003, Schmidt et al. 2003, Snyder and Ives 2003, Crowder et al. 2010). This work shows how specialist aphid predators may benefit from increased amounts of green spaces in urban environments, and given the worldwide decline of specialist species (Clavel et al. 2011, Le Viol et al. 2012), and their sensitivity to habitat changes (Devictor et al. 2008), it would be advantageous to continue the survey of functional composition of communities (Lizée et al. 2011), which would allow park managers to evaluate in real time the impact of urban planning and green area management on ecosystem functioning promoted by beneficial arthropods.

Chapter 6 DOES URBANISATION AFFECT THE OUTCOME OF COMPETITION BETWEEN TWO HERBIVORES?

6.1 INTRODUCTION

The ecological consequences that arise from the rapid growth of urban areas around the world are likely extending outside cities limits (Bradley and Altizer 2007, Grimm et al. 2008). The fragmentation and isolation of habitats, the alteration of regional and local climates, the introduction of non-native species and alterations of bio-geochemical cycles and processes which usually occurs in urban areas (Grimm et al. 2008, Bang and Faeth 2011), is affecting not only the diversity and abundance of arthropods, but also interactions between species that dictate community stability and food web structure (Didham et al. 1996, Faeth et al. 2005, Clark et al. 2016, Turrini et al. 2016).

Competition is regularly cited as one of the main factors that affect patterns of composition of ecological communities (Kelt et al. 1995, Begon et al. 2006, Kaplan and Denno 2007). And it is hypothesised that ecological communities could be structured by competition occurring directly between species as they compete for resources, or also indirectly due to the action of intermediary species (Denno et al. 1995, Bonsall and Hassell 1997). Competition for food is a dynamic direct interaction between two organisms (same species; intraspecific competition) or between two species (interspecific competition) while foraging on the same resource (Petren and Case 1996). It is challenging for ecologists to stablish the direct and indirect ways that urbanisation influences food web dynamics and ecological interactions (Faeth et al. 2005), and it is assumed that it could move the structure of some populations towards an over-abundance of weak competitors (Anderies et al. 2007), because at high disturbance levels, coexistence mechanisms could fail if predation pressure is abnormally reduced in those areas (Shochat et al. 2010).

Basic models that form the base of our understanding of the dynamic of species interactions and coexistence usually presume that interactions are governed and mediated only by fundamental characteristics of the two interacting species and consequently are only dictated by their densities (Werner and Peacor 2003). However, if phenotypic changes occur when an organism encounter a potential competitor, this trait alteration might potentially have a per capita effect on fitness and population density on both the reacting species and the other species (Werner and Peacor 2003). Competition can also be mediated indirectly through predators and other natural enemies, such as parasitoids and pathogens (Hudson and Greenman 1998, Müller and Godfray 1999, Van Veen et al. 2008), and the most known example is apparent competition, in which the presence of one species leads to higher densities of a common natural enemy, which consequently causes increased mortality and a lower population density of a second species (Holt 1977, Holt and Lawton 1993, Bonsall and Hassell 1997, Muller and Godfray 1997, Van Veen et al. 2008).

Competition can also be mediated by mutualists, when the species which engage a mutualist interaction with other organisms may have an advantage in fitness and performance in relation to the second species exploring the same food resource (Müller and Godfray 1999, Engel et al. 2001, Urcelay and Diaz 2003). Another factor that also might alter the outcome of competitive interactions which is rarely taken into account on the literature is environmental variability, which can play an effect on abundance of natural enemies, as well as in the performance and fitness of the competing species and the strength of their interactions with other organisms (e.g. host plants, predators, mutualists, parasites and pathogens) (Chesson and Warner 1981, Persson 1993, Gonzáles et al. 2002, Staley et al. 2007).

There are very few studies about the effect of one competing species over another is influenced by increasing levels of perturbations and heterogeneity that occur in urban environments, as well about the importance of factors that can mediate (promote or diminish) interspecific competition including host plants, natural enemies and mutualists (Denno et al. 1995, Kaplan and Denno 2007). According to Chamberlain et al. (2014), variation in the outcome of interspecific interactions can be considered common and context dependent, with the sign or magnitude of the effect on fitness or population density varying as a function of the biotic or abiotic context in which the interaction happen. Unfortunately, the role of habitat and other indirect interactions in mediating competition is often unrecognised by the literature (Engel et al. 2001, Van Zandt and Agrawal 2004, Viswanathan et al. 2005). For that reason, we must examine a wider perspective that takes intermediated trophic links into consideration when studying interspecific competition (Kaplan and Denno 2007), as well as how relationships between different species can be altered by variation in their habitats.

It is suspected that sap-feeding insects might compete more often than other insects (Moran and Whitham 1990, Denno et al. 1995, Inbar et al. 1995), and competition could be more intense among closely related taxa (Petersen and Sandström 2001). Sap-feeding homopterans like aphids are often sedentary and thus cannot move great distances to escape the effects of competition (Karban 1986, Moran and Whitham 1990). Here, we characterize the interaction occurring between the regularly ant-attended black-bean aphid *Aphis fabae* Scopoli (Hemiptera: Aphididae) (Völkl et al. 1999, Fischer et al. 2001, Fischer et al. 2005), and the non-ant attended pea aphid *Acyrthosiphon pisum* Harris (Hemiptera: Aphididae) (Engel et al. 2001), both reared on broad bean plants *Vicia faba* L. We controlled plant quality in order to consider only interactions at higher trophic levels and abiotic environmental variables related to increased degrees of urbanisation. Colonies were placed on an urbanisation gradient in a large town in southern England, and we used this system to test if urbanisation influences the interaction between two coexisting herbivores sharing the same resource, and how this interaction is mediated by their natural enemies, mutualists, and variation on urban habitat variables.

6.2 METHODOLOGY

6.2.1 STUDY AREA AND HABITAT VARIABLES

The study area is located in Greater Reading, Berkshire (51°27’N, 0°58’W), a large town in southern England with a population of 290 000, which comprises an area of ca. 72km^2 (Office for National Statistics 2013). We selected a range of study sites that followed an urbanisation gradient from suburban gardens and housing areas on the south, until sites located in the town center, covering a range of different urban habitats like parks, churchyards, carparks, public and private gardens. Thirty-two study sites were selected and each site was a least 110 meters apart.

Through geoprocessing methods using QGIS 2.8.1 (QGIS Development Team 2015), habitat variables from each study site were derived from the Ordnance Survey MasterMap® Topography layer, which represents topography at a scale of 1:1250. In each study site 50 meter radius buffers were delimited, and then a reclassification of vectors was performed to result in proportions of area of impervious surfaces, which was composed of buildings (any building or artificial structures made of concrete, brick or stone) and byways (roads, roadsides, tracks or paths made of impervious surfaces such as asphalt).

6.2.2 EXPERIMENTAL APHID COLONIES AND SAMPLING

Source aphid colonies of *Acyrthosiphon pisum* Harris (hereafter PA) and *Aphis fabae* Scopoli (BB) were maintained in the laboratory using plastic and mesh cages. Cultures were kept at a constant temperature of 20 ± 1 °C and 16:8 h light regime at ambient humidity on broad bean, *Vicia faba* L. (var. the Sutton dwarf). For the experimental aphid colonies *Vicia faba* L. plants were sown 22 days before being disposed in the field, in pots with potting compost (Vitax Grower, Leicester, England), being watered as needed. Three days before the experimental colonies being allocated to the study sites, adults from the source aphid colonies were transferred and reared on the broad bean plants (18-22 cm in height), to allow new colonies to become established. To evaluate aphid competition, we followed the approaches of Gianoli (2000) and Mooney et al. (2008), with treatments being consisted by aphids placed on their host plants either alone or in combination, so each study site had three plants with aphid colonies as follows: three adults of PA (single PA treatment) on one *Vicia faba*, three adults of BB on one *Vicia faba* (only BB treatment), and three adults of PA and another three of BB on one *Vicia faba* (PA competing treatment and BB competing treatment). Two days after treatments were disposed in the field aphid, ants and predator numbers were recorded. The next sampling records happened every four days for additional four times.

According to Salyk and Sullivan (1982) BB aphid*,* living on *Vicia faba*, changes its feeding site from the stem to the leaves, and from the upper to the lower surface of leaves, when PA is also present. Kunert et al. (2008) and Dixon and Agarwala (1999) found that BB do not produce winged offspring in the presence of natural enemies, in contrast to results for the PA, however, colonies of BB responded to an increase in aphid density by increasing winged morph production. So to see if there is any indication of behavioural interference between the two species, the treatments with PA and BB aphids on the same plant will be additionally observed for changes in feeding sites and winged offspring production on either species. This experiment occurred between 26th of July until 14th of August of 2016.

6.2.3 DATA ANALYSIS

The dataset used to analyse differences between treatments consisted of numbers of aphids and predators and presence or absence of ants on each aphid treatment in each of the five recording events. To analyse aphid colony numbers we used a zero-inflated generalized linear mixed model fitted by maximum likelihood, with a negative binomial error distribution family and log-link function (Crawley 2007, Zuur et al. 2009) using package glmmADMB (Skaug et al. 2014) in the R 3.1.2 environment (R Development Core Team 2014). The model started considering all three-way interactions between fixed factors (treatment, aphid species, proportion of impervious surfaces, predator abundance and occurrence of ants), and as we expected a positive relationship between presence of ants and higher proportions of impervious surfaces that was found in previous chapters, we also allowed for a four-way interaction between treatment, species, ant occurrence and proportion of impervious surfaces as well. In this analysis, a significant interaction between species, treatment and other ecological factors would indicate that the relative strength of competition depends of these factors (Mooney et al. 2008, Smith et al. 2008). As the same set of sites were sampled in five different days, as well as treatments which belonged to the same study site will be more correlated with each other in comparison with treatments in other locations, treatment within sites within date was considered as a random factor in this model. Model simplification was made via hypothesis testing through analysis of deviance tests, where the full model is initially fitted and subsequently all allowable interactions and terms are dropped by comparing nested models until the final model is found (Crawley 2007, Zuur et al. 2009). Unfortunately some plants were lost during the experiment due to plant herbivory by slugs and snails and damaging by the public, this way we had 612 observations for analysis.

6.3 RESULTS

We observed 1126 aphids and 66 predators on PA single treatments, 3740 and 73 predators on BB single treatments, 1127 PA aphids and 2462 BB aphids with 103 predators on the mixed treatments. Figure 6.1 shows the general number of aphids for each species and treatment on each counting event. Ants found on both treatments were

Myrmica rubra (L.) and *Lasius niger* (L.). Predators were composed by spiders (Arachnida; 45%), hoverfly larvae (Diptera: Syrphidae; 34%), aphid midges (Cecidomyiidae; 9%), ladybirds (Coleoptera: Coccinellidae; 6%), earwigs (Dermaptera: Forficulidae; 2%), lacewings (Neuroptera; 2%), flower bugs (Hemiptera: Anthocoridae; 1%), and in smaller amounts of harvestmen (Arachnida) and damsel bug (Hemiptera: Nabidae). The mean proportion of impervious surfaces on the study sites ranged from 0 to 0.77 (mean ± SE: 0.38 ± 0.02).

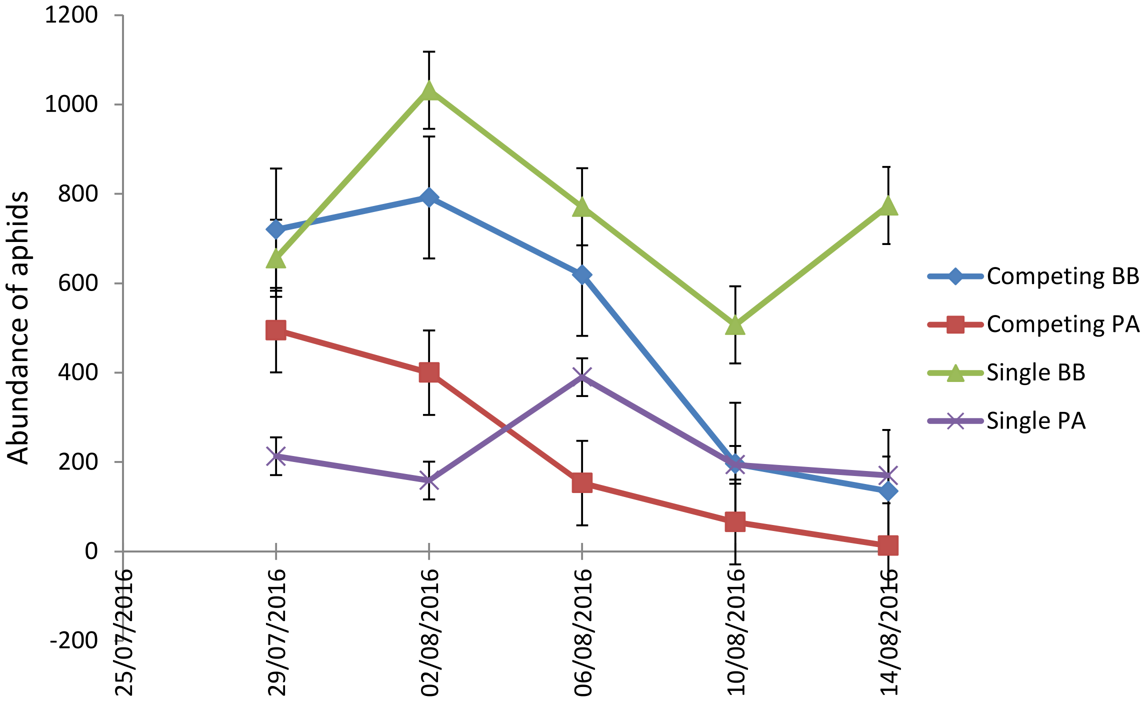


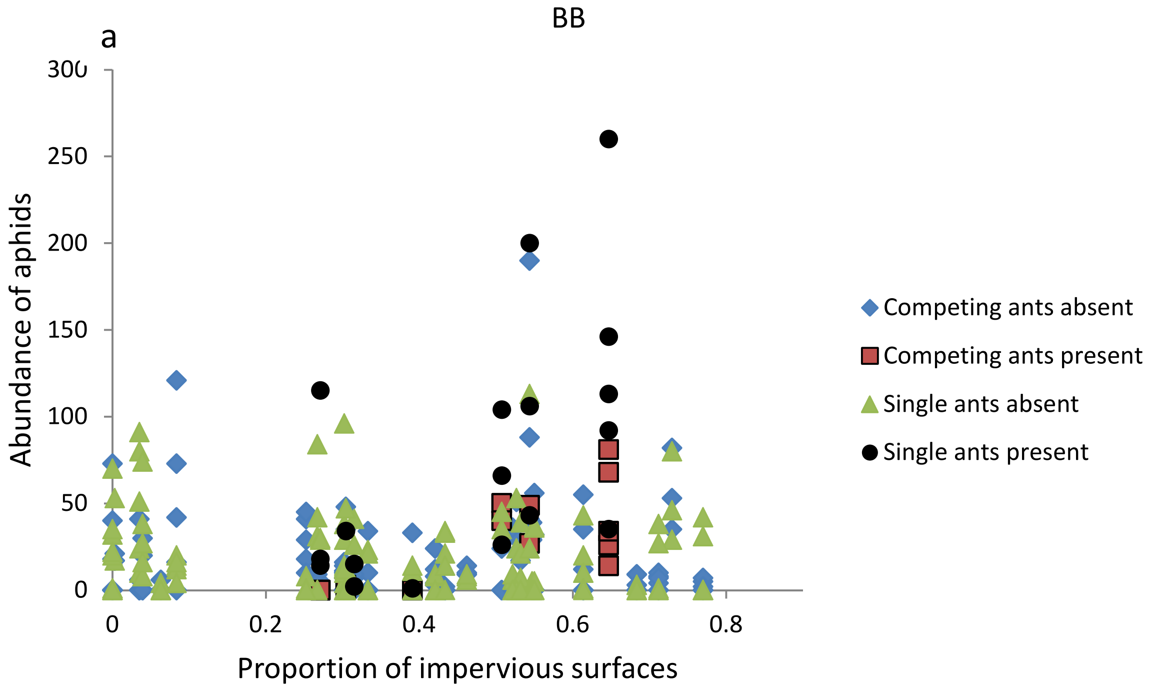
FIGURE 6.1. General abundances of *Acyrthosiphon pisum* (PA) and *Aphis fabae* (BB) species on each treatment per day of sampling. Bars show standard errors.

Presence of winged offspring production was only observed on PA species on mixed treatments, however it was only noticed during four occasions in four different sites (proportion of impervious surfaces: 0, 0.28, 0.30, 0.39). A difference in preference of feeding sites on the plant within the same species in different treatments (single or combination) was not observed. Table 6.1 shows the best model in explaining abundance of aphids in different treatments and its relation with other explanatory variables. The competition treatment generally had lower aphid numbers, and BB aphids had higher numbers in comparison to PA aphids. Presence of ants on aphid colonies generally had a negative effect, and numbers of predators were positively correlated with aphid numbers, suggesting a density dependent relationship also found in previous chapters. The interaction between competition and amount of impervious surfaces in the habitat showed to have a positive effect on aphid numbers, however the interaction between competition and predators appeared to have a negative effect (borderline significant). Although BB aphids had overall higher numbers than PA aphids, its population numbers appeared to be negatively correlated to the amount of impervious surfaces in relation to PA aphids. However when ants were present in colonies BB aphids had increased population numbers (interaction between BB species and presence of ants), and lastly, the interaction between presence of ants and amount of impervious surfaces were positively correlated to aphid numbers (Table 6.1, Figure 6.2).

TABLE 6.1. Results of generalised linear mixed effects model that compare aphid abundances of two aphid species living in broad bean plants singly or in combination. Significant terms and interactions are shown in bold. Treatment: factor of two levels (competing or single); Aphid sp: factor of two levels (BB or PA); Ants: factor of two levels (presence or absence); Predators: continuous explanatory variable; Impervious surfaces: proportion of impervious surfaces within 50 m radius buffers surrounding each study site.

Response variable	Fixed effects	Estimate ± SE	Z	P
Aphid N	**Intercept**	**1.26 ± 0.640**	**1.97**	**0.049**
	Treatment_comp	**-1.715 ± 0.407**	**-4.21**	**2.50E-05**
	Aphid sp_BB	**1.252 ± 0.274**	**4.57**	**4.90E-06**
	Impervious surfaces	-0.817 ± 0.697	-1.17	0.242
	Ants_Presence	**-3.821 ± 1.505**	**-2.54**	**0.011**
	Predators	**0.633 ± 0.214**	**2.95**	**0.003**
	Treatment_comp x Impervious surfaces	**2.710 ± 0.870**	**3.12**	**0.002**
	Treatment_comp x Ants_Presence	-1.052 ± 0.803	-1.31	0.190
	Treatment_comp x Predators	**-0.505 ± 0.259**	**-1.95**	**0.051**
	Aphid sp_BB x Impervious surfaces	**-1.261 ± 0.578**	**-2.18**	**0.0292**
	Aphid sp_BB x Ants_Presence	**3.676 ± 0.832**	**4.42**	**9.90E-06**
	Impervious surfaces x Ants_Presence	**7.388 ± 2.393**	**3.09**	**0.002**
	Ants_Presence x Predators	1.574 ± 0.881	1.79	0.074
	Treatment_single x Aphid sp_BB x Predators	-0.307 ± 0.239	-1.28	0.199
	Treatment_comp x Aphid sp_BB x Predators	0.250 ± 0.150	1.67	0.095
	Treatment_comp x Ants_Presence x Predators	-0.936 ± 0.812	-1.15	0.249
	Aphid sp_BB x Ants_Presence x Predators	-1.388 ± 0.827	-1.68	0.093

The analysis of deviance indicated that we should take out interactions from the full model between treatment, species, impervious surfaces and occurrence of ants (D= 0.82, df= 1, P= 0.365) and also the interaction between treatment, species and impervious surfaces (D= 1.5, df= 1, P= 0.221), on the model simplification process. Figure 6.2 shows the distribution of aphid abundances according to species and treatments in relation to the amount of impervious surfaces in the habitat when ants were present or absent.



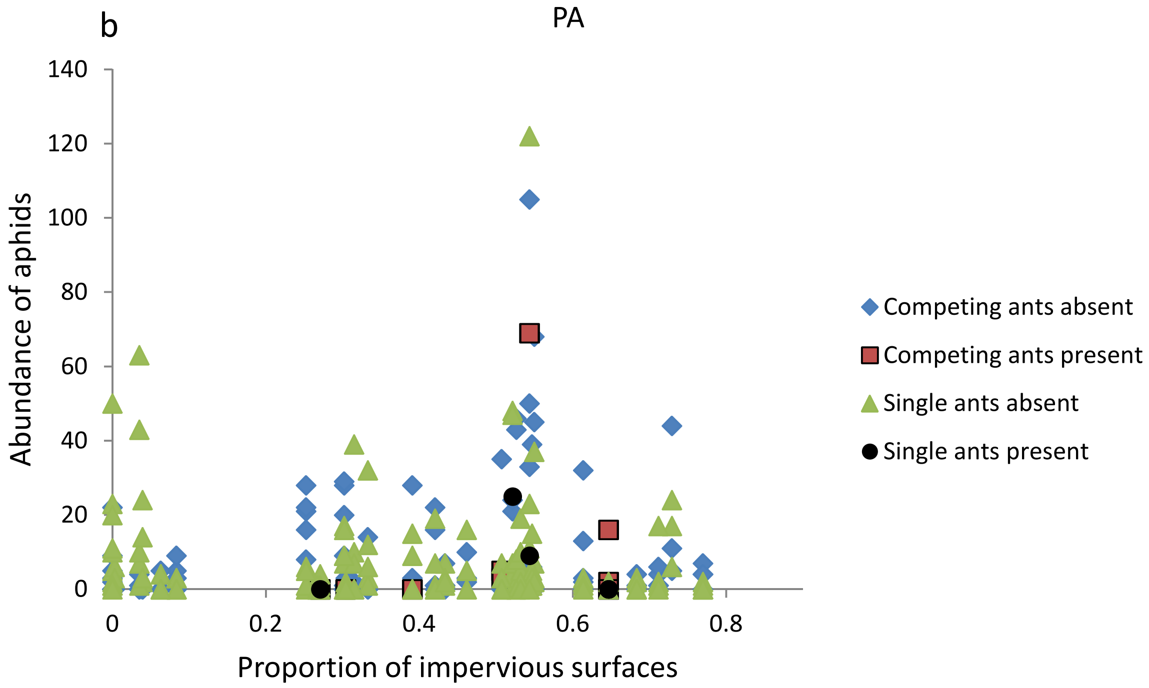


FIGURE 6.2. Abundance of *Aphis fabae* (BB, panel a) and *Acyrthosiphon pisum* (PA, panel b) in relation to the amount of impervious surfaces on the study sites, in single or competing treatments with ants present or absent**.**

6.4 DISCUSSION

The objective of this work was to investigate if urbanisation disrupts the outcome of a competitive interaction, and if this interaction could also be mediated by natural enemies or mutualists. In the analysis performed, we would expect to see a significant interaction between the species evaluated, treatment (single or combination) and the other explanatory factors of interest (urbanisation, mutualists and predators), which we did not. However, some trends on the data show some indication it might; therefore we state our results as inconclusive probably because of lack of explanatory power.

From our model, the competition treatment had significantly lower numbers of aphids, and black bean aphids showed generally higher population numbers than pea aphids. For us to support our hypotheses that the strength of the interspecific competition between the two species is affected by urbanisation and/or is mediated by natural enemies and mutualists, we would have found a significant interaction between these explanatory factors. However, when evaluating the other significant explanatory terms like presence of ants increasing BB aphid numbers, a positive significant interaction between ants and amount of impervious surfaces and also from observing the distribution of data of BB aphids singly and in combination when ants were present (Fig. 2a), we can almost see that ants appear to improve the reproductive rate capacity of the already “competitive superior” BB aphids in highly urbanised sites. Unfortunately, the interaction between BB species, treatment, impervious surfaces and presence of ants was not significant and was the first term to be removed in the model simplification process. We attribute this to the fact of the general lower numbers of study sites that had ants present that could play an effect strong enough for a significant interaction between all these explanatory variables to be detected on our analysis.

On previous chapters, we also found a significant correlation between occurrence of ants and increased population numbers of BB colonies and also how urbanisation appears to benefit this mutualistic relationship, which could potentially lead to an increase in populations of ant-attended pest species in these areas. Other studies have also found that the intensity and occurrence of mutualistic interactions can be strongly dependent on the physical and biological location in which they happen (Cushman and Whitham 1989, Cushman and Addicott 1989, Chamberlain et al. 2014, Mooney et al. 2016). Our data shows that general numbers of BB aphids have a negative correlation to the increased amount of impervious surfaces on the habitat (even though their numbers are still higher than PA numbers); however, the presence of the mutualist relationship with ants appears to dramatically change that. Chamberlain et al. (2014) showed that mutualism and competition were the interactions types most likely to present context dependency, with magnitude and sign of the interactions varying most along spatial and abiotic gradients. This leads us to agree with previous findings that mutualists have the potential to act as “third parties”, potentially mediating the effects of predation, herbivory and maybe also competition, by altering the consequences of these antagonistic interactions on community structure in changing environments (Melián et al. 2009, Clark et al. 2016).

In our model, we also observed a positive interaction between the competition treatments and proportion of impervious surfaces. We believe this significant positive interaction majorly comes from the variation of the competition treatment of BB species, where the variance of the data appears to be positively associated to the increase amount of impervious surfaces (in both presence and absence of ants, Fig 2a). One possible explanation to this trend could be attributed to an effect know as apparent competition, which is an indirect interaction defined as a reduction in the population density of one prey species when that of another prey species increases, with the interaction mediated by an increase in predation (Holt and Lawton 1993, Bonsall and Hassell 1997, Alhmedi et al. 2011), which can occur whether or not the two species directly compete for the same resources (Holt 1977, Morris et al. 2004). There is an indication of this effect on the model on the positive relationship between aphid numbers and the interaction between competition, BB aphids and predators (however not significant), in which somehow could be stronger in highly urbanised sites. We are aware that with the present data is not currently possible to draw clear conclusions about the causes and the ecological significance of this trend, however we would like to discuss this possible explanation given the already recognized importance of natural enemies in being able to affect and regulate insect populations due to apparent competition, and also because it can produce patterns in communities that resemble those caused by resource competition (Holt and Lawton 1993, Bonsall and Hassell 1997, Muller and Godfray 1997, Hudson and Greenman 1998, Juliano 1998, Morris et al. 2004).

A clear next step in our research is try to quantify more accurately how urbanisation can potentially affect interspecific competitive interactions between closely related species. Our current data suggests that the main effect is through mediation of competition by mutualists in highly urbanised habitats, however is also possible that variation in abiotic features in the environment might also impose an effect on fitness and therefore in the competitive relationship between species as habitat variation occurs. As an example, *Aphis fabae* is known to have its population growth stimulated by air pollution (Dohmen et al. 1984, Flückiger 1987), and *Acyrthosiphon pisum* was found to be negatively affected by artificial light at night (Bennie et al. 2015). Competitive exclusion has being claimed as a driver of urban diversity loss (Shochat et al. 2006, Shochat et al. 2010, Farwell and Marzluff 2013), thus a mechanistic understanding about how some direct effects of urbanisation and indirect effects of predation and mutualism can mediate and influence a competitive interaction between species might help us to disentangle one of the many process that might lead to diversity loss in human-dominated environments.

Chapter 7 GENERAL DISCUSSION

7.1 MAIN FINDINGS AND CONTRIBUTIONS TO THE FIELD

This work, “The ecological consequences of urbanisation”, describes my investigations into the many complex ways that populations, community structure and species interactions are affected by the novel habitats created by city growth.

In Chapter 2, I explored the local and fine scale environmental drivers of naturally occurring aphid communities, and their coccinelid and syrphid predators in urban gardens. Gardens form an important component of green spaces in towns and cities, and may help to reduce urbanisation impacts by serving as refuges to plants and animals. Aphids, hoverflies and ladybirds are surprisingly little investigated in relation to urban habitats, and by focusing in both trophic groups at once (herbivores and predators), they can help indicate the health of valuable ecosystem services in urban gardens.

I observed 45 aphid species (4 of them exotic), 17 hoverfly species and 9 ladybird species (including the invasive *Harmonia axyridis* Pallas). I found that aphid richness and abundance was positively correlated with host plant abundance and garden plant species richness. Hoverfly abundance was only positively and significantly correlated to garden plant richness, both aphidophagous species and in general, while the abundance of ladybirds were significantly and positively correlated to aphid abundance and garden plant species richness, and negatively associated to the proportion of impervious surfaces. Although the obvious detrimental effect of locally increased urbanisation to ladybirds as a group, the fact that the groups investigated did respond to the local factors investigated (garden plant richness and host plant abundance) indicate that garden owners are able to make decisions that effectively help onto the promotion of urban wildlife conservation and the resilience and persistence of healthy ecosystem services in cities (Philpott et al. 2014). I also considered how gardens might be an important source for environmental education towards conservation which is often unrecognized. Our main contribution to the field of urban ecology from this chapter is the investigation on patterns of aphid diversity in urban gardens, which I believe this work was the first to address. Also, studies that evaluated trends in abundance and richness of herbivores and predators at the same time in urban settings are quite limited (but see e.g. Denys and Schmidt 1998, Christie et al. 2010, Philpott et al. 2014), and to our knowledge this was the first work to examine these patterns on this specific system (aphids – hoverflies – ladybirds) in urban greenspaces.

In Chapter 3, using experimental colonies of the black bean aphid *Aphis fabae* Scopoli reared on *Vicia faba* L, I asked if patterns of predator-prey, host-parasitoid and ant-aphid mutualisms varied along an urbanisation gradient. For that, I recorded the presence of naturally occurring predators, parasitoid wasps and mutualistic ants together with aphid abundance in experimental colonies during the summer of 2015. I examined how biotic (green areas and plant richness) and abiotic features (impervious surfaces and distance to town centre) affected (1) aphid colony size, (2) the likelihood of finding predators, mutualistic ants and aphid mummies, and (3) how the interplay between these factors affected patterns of parasitoid attack, predator abundance, mutualistic interactions and aphid abundance. From my results I could see that mutualistic ants reduced predation rate, increased parasitoid attack, and overall drove colonies who engaged in mutualistic interactions to perform better. These findings were not unexpected and were already supported by the literature (Völkl 1992, Kaneko 2002, Kaplan and Eubanks 2002, Tegelaar et al. 2013, Yao 2014). In particular, our results showed similarities with the observations made by Wimp and Whitham (2001), who examined the mechanisms that determined insect community structure in a riparian zone, in which a negative effect of ant presence on generalist predators, while a positive effect on specialist enemies, was also observed. A novel and interesting outcome found by this chapter was that aphid predators responded negatively to the proportion of impervious surfaces, while the remaining trophic groups appeared to be unaffected. To our knowledge, this work presents the first effort to address the interplay between different trophic groups composed by herbivory, predation, parasitism and mutualism concurrently perform in an urbanisation gradient. The findings on this chapter highlighted the variable effects of urbanisation when interspecies interactions are considered and the importance of understanding these to promote efforts to maintain ecosystem services.

When moving further into Chapter 4, I focused on how patterns of predator-prey in aphid species attended and not attended by mutualistic interactions are affected by urbanisation. I assessed how aphids and their associated predators and mutualistic ants occur and are correlated to the main land uses that compose cities (gardens, woodlands, roads and buildings) as well as plant richness of urban green areas. To date, there is no knowledge on how patterns of interactions between herbivores, mutualists and predators, might change and be affected by variance in habitat structure that occurs in cities. There are some studies, however, that previously tested direct and indirect effects of warming on aphids, their predators and ant mutualists by experimental field manipulations (Barton and Ives 2014, Marquis et al. 2014). Our study system was composed by colonies of *Acyrthosiphon pisum* Harris and *Aphis fabae* Scopoli, which were placed on an urban gradient. Sampling occurred during two years with frequent visits to study sites. Both aphid species are known to suffer heavy predation by several predators (Rotheray 1989, Losey et al. 1997), but as opposed to *A. pisum*, *A. fabae* is known to be regularly ant-attended. El-Ziady and Kennedy (1956) demonstrated that the ant *Lasius niger* Linnaeus attending *A. fabae*, accelerated the rate of multiplication and growth of the aphid colony and decreased the proportion of winged individuals among the adults. These ants showed "ownership behaviour", acting aggressively towards intruders such as ladybirds and hoverfly larvae. However, *Lasius* species regularly prey on aphids of non-myrmecophilus species (Engel et al. 2001, Offenberg 2001). As such, I wanted to explore how urban habitats features and plant richness can mediate interactions between these two different colonies, as well as predators and ants associated with it, given the ownership behaviour of ant attending *A. fabae* against its predators, and also the potential competitive interspecific interaction of ants that prey on *A. pisum* against other predatory species.

I believe this work was the first attempt to investigate how aphid colonies differentially attended by ant mutualists simultaneously perform, and how this performance might be affected by changes in their surrounding environment. Some of the new findings that I encountered are when ants act as predators, their numbers are higher in more urbanised habitats, and when they act as mutualists, they are more likely to attend colonies in areas with more plant diversity. I hypothesised that this pattern might be a result of differential behaviour of predatory ants in highly urbanised habitats with poorer food choices, when being directed to predation instead of mutualism when facing an increased need for prey and protein rich food sources. This interesting outcome, however, needs to be confirmed by future investigations.

In contrast to ants, in Chapter 4 I again detected that aphid predator occurrence was reduced in highly urbanised habitats. Although amply hypothesized (Frankie and Ehler 1978, McIntyre 2000, Shochat et al. 2006, Shrewsbury and Raupp 2006, Raupp et al. 2010, Faeth et al. 2011, Burkman and Gardiner 2014, Lowe et al. 2016) only few other studies have experimentally observed reduced numbers of arthropod predators or predation services in urban environments (e.g. Rango 2005, Dale and Frank 2014, Turrini et al. 2016). I discussed how this imbalance on the effect of environmental disturbance on predation in urban habitats could bring important consequences at the community-level assembly in these areas, mainly by disrupting the strength and effectiveness of top-down forces. Also, I concluded that the reduction in predator occurrence, with a concurrent increase in ant presence, could lead to a potential increase in populations of ant-attended pest species in cities, and maybe further impacting the environmental services predators provide in these environments. In addition, I suggested that might be advantageous to investigate with future experimental work whether pest suppression performed by ants on non-myrmecophilous aphid species outweigh the negative impact of ants on other predators.

Given the negative effect of urban habitats on aphid predators detected by previous chapters, on Chapter 5 I decided to explore if there is a differential response of predator functional groups to urban green spaces. There are some examples of studies that utilised the specialists/generalist concept applied to evaluate habitat sensitivity and biotic homogenisation of predator groups to urban environments (e.g. for urban birds, Sorace and Gustin 2009). However, I could not find any other that specifically evaluated the response of the whole community of predators actually found feeding on a particular prey, and classifying it according to the specificity of the predators' dietary breadth in relation to that prey. I believe that my approach avoids the potential biases and confounding effects associated with arbitrary specialist/generalist classifications, which are based on groupings of predator dietary breadth in relation to a wide range of potential prey present in a biological community (Suarez and Case 2002, Attum et al. 2006, Mennechez and Clergeau 2006, Rand and Tscharntke 2007). In general, I expect that specialist predators would be directly linked to the presence of specific prey species, contrasting with generalist species that can rely on a much wider diet. To confirm this I aggregated the whole community of predators found on both aphid species of the previous chapters, and then I classified them according to how important aphids are in their diet: obligatory or aphid-specific predators, which depend on aphids for food; or generalist aphid predators, which are facultative or polyphagous predators in which aphids are just part of a much varied diet. This way, in this chapter I hypothesized that the numbers of specialist predators would be correlated to increased proportions of green spaces in urban habitats, while the abundance of generalists should not be strongly affected. I expected this outcome due to the fact that higher amounts of green spaces in urban habitats will probably lead to also a higher chance of finding specific prey species, which in turn also will lead to a higher chance of finding specialist predators. In fact, from my results I could observe that urbanisation is more detrimental on specialist predators, which abundance were positively and strongly correlated with the amount and size of green spaces. I then discussed the consequences of community simplification and homogenisation in urban habitats, and how the creation and maintenance of green areas within cities should keep being encouraged.

Given the absence of studies in the literature that specifically addressed how competition between two different species might be indirectly mediated through variance on the environment, coupled with interactions with natural enemies and mutualists, in Chapter 6 I wanted to understand which factors of urban habitats have a greater influence the outcome of interspecific competition, by empirically testing if urbanisation determines the interaction between two coexisting herbivores sharing the same resource, and how this interaction is mediated by their natural enemies and mutualists. I could see again some indication of the importance of mutualistic ants as a force in determining the dynamics of two aphid species competing for the same resource, and how this dynamic might change synergistically as the environment become more urbanised. Although our results were not conclusive, I believe that future investigations with increased replicate sites – especially those with presence of mutualistic ants – might address conclusive and significant responses of how urbanised environments might mediate competitive interactions through indirect effects on the presence and strength of herbivore, mutualists and predator interactions. Also, the results reported in this chapter and Chapter 5 emphasise how ants, with their multiples roles in food web dynamics and species interactions, are key ecological agents of both natural and anthropogenic systems (Sanders and van Veen 2011, Meyer et al. 2013).

I believe that my main and most important contribution to the field of urban ecology is through addressing how herbivore numbers, mutualistic interactions, and predation concurrently influence each other in response to environmental heterogeneity resulting from the transformational effects of urbanisation. Furthermore, my work draws attention to the detrimental effects that increased urbanisation plays on predators in comparison with other trophic guilds, on which experimental work on this subject is still particularly lacking. Although I only focused on arthropods and local and fine scale environmental factors, I believe my focus was most advantageous to the field when considering the lack of studies and gaps of knowledge about trophic dynamics and species interactions in urbanised environments, which questions are only appropriately addressed by selecting the proper habitat scale in which it occurs. Additionally, our study system (aphids, their predators, mutualists and parasitoids) is regarded as of great interest, mainly because of the impacts to crops caused by aphids, causing hundreds of millions of dollars in lost production each year (Oerke et al. 2012), and also the benefits of pest suppression and control carried out by predators and parasitoids (e.g. ladybirds, hoverfly larvae and parasitic wasps) and pollination (hoverfly adults). I therefore hope that my work could also be of value to the field of biological control in agroecosystems.

7.2. FUTURE DIRECTIONS IN URBAN ECOLOGY

Urban ecologists have now a great opportunity to apply interesting evidence-based research to help create biological diverse and sustainable cities for the next generations (McDonnell and Hahs 2013). The evolution of our ecological knowledge about the function and structuring of biological communities living in urban areas has improved our understanding of basic ecological principles, and it has also provided us with opportunities to gather valuable information that might help us to improve the health of urban ecosystems (McDonnell and MacGregor-Fors 2016). Just as any other biological system, cities depend on ecosystems services to sustain long-term conditions for quality of life (Gómez-Baggethun and Barton 2013). Additionally, cities serve as important living laboratories that present possibilities to test fundamental ecological questions, such as the effect of landscape fragmentation on the distribution of organisms, the effect of night lighting on the circadian rhythms of humans and other organisms, behavioural changes to increased noise and pollution, changes in migration and reproduction, and the role of urban green spaces in providing ecosystem services to urban dwellers (McDonnell and MacGregor-Fors 2016). All these questions still need to be fully addressed to a range of different organisms and systems that even now remain under investigated, particularly in urban areas in the tropics, where the field of urban ecology remain at its first steps.

Moreover, urban ecosystems remain largely ignored by ecosystem service research (Gómez-Baggethun and Barton 2013). The interest given to valuing services like water filtration and supply, pollination, pest suppression and nutrient cycling is still relatively modest in comparison to that in other ecosystems like forests or wetlands (Gómez-Baggethun and Barton 2013). If agroecosystems primarily provide us food from crops and pasture, oceans and forests afford carbon sequestration and climate regulation and wetlands maintain the cycling of nutrients, urban ecosystems provide crucial services that directly affect human population’s health and security such as noise reduction, degradation of pollutants, climate regulation, air purification and runoff drainage (Bolund and Hunhammar 1999, Mentens et al. 2006, Gómez-Baggethun and Barton 2013).

Valuation on ecosystem services can therefore better inform decision makers and governments towards better decisions and priority-setting in urban planning.

Also, progress towards the development of effective conservation methods for mitigation of impacts of urban areas on wildlife needs to be highly encouraged and expanded, and one admirable example of such actions are the measures implemented for mitigation of impacts developed from studies on the field of road ecology, such as installation of wildlife road-crossing structures already undertaken in Australia, Europe and North America (Langton 2002, LaPoint et al. 2003, Taylor and Goldingay 2010), as well as the development of GIS-based information technologies that help to evaluate the permeability of motorway networks to provide recommendations for existing and future roads and highways that ensure landscape connectivity across different taxa (Woess et al. 2002, Hlaváč 2005). However, some difficulties encountered in the development of such projects are due to several factors, including the unfamiliarity that many conservation scientists have with urban landscapes, and the need to identify and incorporate factors of an urban area's uniqueness into biodiversity conservation projects (Parker 2015). But even with such impediments, we still have great examples of successful projects carried out in urban environments, like canopy overpasses for brown howler monkeys (*Alouatta guariba clamitans* Cabrera) to increase movement between urban forest remnants and to protect from electric hazards and road-kills in southern Brazil (Teixeira et al. 2013). According to Parker (2015), by considering a wide perspective about ecosystems and the knowledge already available by urban ecology studies when working in project on areas that include urban spaces, and utilising technological and other resources readily available within cities, might help to effectively incorporate robust information about management frameworks on implementation efforts for biodiversity conservation in urban ecosystems.

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